

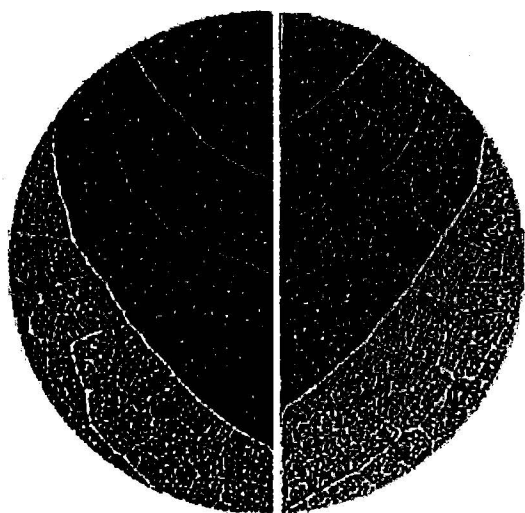
III Taller Sobre la Bioecología y Manejo del Salivazo de los Pastos

23 - 27 octubre de 2000

Centro Internacional de Agricultura Tropical (CIAT)
Cali, Colombia

LECTURAS

Compiladas por Daniel C. Peck
Centro Internacional de Agricultura Tropical (CIAT)



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LECTURAS

Biología y Comportamiento:

Fewkes 1969a

Kuenzi y Coppel 1985

López et al. 2001

Peck 1998

Peck 2000

Whittaker 1970

Peck 2000

Pires et al. 1993

Cría:

Lapointe et al. 1989

Peck et al. sometido

Impacto:

Byers y Wells 1966

Holmann et al. en preparación

Valério y Nakano 1988

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Hewitt 1989

Diversidad y Distribución

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Peck et al. sometido

Manejo:

Cardona et al. 1999

Fewkes 1969b

Lapointe et al. 1992

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Ecología Poblacional:

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Phytotoxemia of Coastal Bermudagrass Caused by the Two-Lined Spittlebug, *Prosapia bicincta* (Homoptera: Cercopidae)¹

R. A. BYERS² AND HOMER D. WELLS³

ABSTRACT

An adult two-lined spittlebug, *Prosapia bicincta* (Say), causes phytotoxemia of Coastal bermudagrass, a cultivar of *Cynodon dactylon* (L.) Pers. Symptoms appear as White stipple and Ivory to Sea Foam streak of leaves and browning and dying of the entire above ground portion of the plant. Disease severity is correlated with the degree of infestation and length of feeding time on the host. Some symptoms developed after 1 spittlebug was confined to a stem for only 1 hr. Nymphs, in any of the 4 instars, were incapable of producing visible symptoms. Histological studies revealed that the nymphs and the

adults feed in the xylem. The toxin appeared to move both up and down the stem in the xylem and escaped through the border parenchyma into the mesophyll in the leaves where it caused loss of chlorophyll and, later, death of both parenchyma and mesophyll. Confining an adult to the middle portion of a stem resulted in leaf symptoms both above and below the point of confinement. Confining an adult to an area above the fork of a divided stem resulted in leaf symptoms both above and below the point of confinement but not on the alternate arm of the fork.

The two-lined spittlebug, *Prosapia bicincta* (Say), caused extensive damage to Coastal bermudagrass, a cultivar of *Cynodon dactylon* (L.) Pers. (Beck 1963, Byers 1965). Since leaf spot and stolen rotting organisms are frequently associated with spittlebug damage on Coastal bermudagrass, we wanted to ascertain if this spittlebug under controlled conditions and in the absence of known disease-producing organisms can produce the typical symptoms that are observed in the field. We wanted to know whether it causes phytotoxemia as described by Carter (1939, 1962) and Leach (1940) or serves as the vector for a virus or other type of pathogenic disease. If this spittlebug causes phytotoxemia, we need to determine the stage or stages in which the toxin is produced and investigate the feeding habits of the insect during its life cycle.

Experiments were conducted in which spittlebugs were reared to the various instars and to maturity on pearl millet [*Pennisetum typhoides* (Burm.) Stapf. & C. E. Hubb.], oats (*Avena sativa* L.), centipede grass [*Eremochloa ophiuroides* (Munro) Hack.], and St. Augustine grass [*Stenotaphrum secundatum* (Walt) Kuntze] and then used as test insects on Coastal bermudagrass. Histological studies were conducted on leaves, stems, and roots of the grass on which nymphs in the different instars and adults had fed.

MATERIALS AND METHODS

Female spittlebugs were collected from the field in October and November and the system described by Byers (1965) was used for procuring eggs for use in these experiments.

Eggs in the eye-spot stage were placed in plastic culture dishes containing young pearl millet sprouts. The eggs hatched within 3 days; on the fourth to seventh days the young nymphs and accompanying spittle masses were transferred to disease-free Coastal bermudagrass, pearl millet, or oats growing in 4-in. clay pots. The pots were covered with tight-fitting aluminum wire cages; then covered with plastic bags, to maintain high humidity; the plastic bags were removed during the nymph's third instar. The clay pots were maintained in individual steel saucers which were kept full of water. Nitrate of soda was added at intervals throughout the period to keep the grasses in a vigorous state of growth. The grasses were cut to a height of 4 in. at frequent intervals. Eggs in the eye-spot stage were placed directly on the base of the plant of centipede grass or St. Augustine grass in 8-in. pots in the greenhouse. The grasses were watered at regular intervals and caged with tight-fitting plastic screen soon after the nymphs entered the 4th instar. Newly emerged adults were confined with an aluminum screen wire cage (1 adult/pot) on disease-free Coastal bermudagrass in 4-in. clay pots in the greenhouse and allowed to feed for various periods (Table 1). Each feeding period was replicated 8 times except the 96- and 168-hr periods, which were replicated 7 and 6 times, respectively.

Nymphs in the first and second instars were transferred to disease-free Coastal bermudagrass grown in 4-in. clay pots in the greenhouse. The nymphs were allowed to mature on Coastal bermudagrass and the adults were removed as they emerged. The plants on which nymphs and adults were confined were observed daily for the development of symptoms which were described and categorized as to types. Maerz and Paul (1930) color charts were used to determine the colors in the description of symptom complexes.

Another test (replicated twice) consisted of 4 adults confined to a single stem of Coastal bermudagrass for 48 hr.

Four adults were confined in small aluminum-wire cages, 1 in. high, for 24 hr to each of the 3 following Coastal bermudagrass stem loci on which leaf sheaths

¹ Cooperative investigations at Tifton, Ga. of the Crops Research Division and the Entomology Research Division, Agricultural Research Service, USDA, and the University of Georgia, College of Agriculture Experiment Stations, Coastal Plain Experiment Station. Published with the approval of the Director as Journal Series Paper no. 230. Accepted for publication January 21, 1966.

² Entomologist, Entomology Research Division, Agricultural Research Service, USDA, Tifton, Ga.

³ Senior Research Plant Pathologist, Crops Research Division, Agricultural Research Service, USDA, Tifton, Ga.

Table 1.—Leaf symptoms of Coastal bermudagrass resulting from confinement of adult *P. bicornis* for varying lengths of time.

No. hr confined	Mean no. of damaged leaves/plant			Duncan's multiple range ^a
	Stippled	Streaked	Brown	
1	0.12	0.37	0.37	a
2	.00	.37	.75	a
4	.25	1.00	.37	a
8	.50	.75	.50	a
16	.00	1.00	.87	a
24	.12	1.37	2.00	b
48	.12	1.00	3.12	b
96	.29	1.28	4.14	c
168	.33	1.16	5.00	c

^a Duncan's multiple range established only for leaves that were brown. Means with same letter not significantly different at P 0.01.

had been removed: (1) from ground level to 1 in. above; (2) 1-in. area in the middle of a simple stem; and (3) 1-in. area above the fork of a divided stem. Each treatment was replicated twice. Patterns of symptom development were observed over a period of 7 days.

Two-lined spittlebug adults were restricted to the base of Coastal bermudagrass stems on which leaf sheaths had been removed. Several days later, the living leaves showing varying symptoms were sectioned by hand (with a razor blade) and studied microscopically to determine the tissues affected. Live portions of stems on which nymphs in each of the 4 instars and the adult had fed were sectioned by hand and examined microscopically to determine the tissue or tissues in which this spittlebug feeds.

RESULTS

No symptoms developed on any of the Coastal bermudagrass on which only nymphs were allowed to feed.

Symptoms developed within 1–3 days after adults began feeding (Fig. 1). The first symptoms appeared on the leaves as White stippled areas, arranged in broken rows parallel to the leaf veins. In many instances, the stippled areas later coalesced to form Ivory (10B2) to Sea Foam Y (17C2) streaks. Some leaves remained stippled or streaked, but the most severe or advanced symptoms so progressed that entire leaves turned Vanilla Brown (10C3) and died. The individual stems on which 4 adults were confined for 48 hr did not become stippled or streaked, but they withered and died within 4 days. The severity of damage was directly proportional to the length of time the adult was confined to the plant (Table 1). Some plants developed symptoms after the adult was confined on them for 1 hr. All plants on which adults were confined for 2 hr and longer developed symptoms. The symptom expression was fully developed by 14 days. In instances where the above-ground portion of the plants was not killed, new leaves appeared above the damaged leaves and were normal in every respect. All plants in which all the above-ground growth was killed developed new normal-appearing growth from the rhizomes.

Plants on which adults had been confined for 24 hr on stems (leaf sheaths removed) within 1 in. of the soil surface developed symptoms on the leaves. Plants on which adults had been confined for 24 hr within a 1-in. length on the middle of the stems (leaf

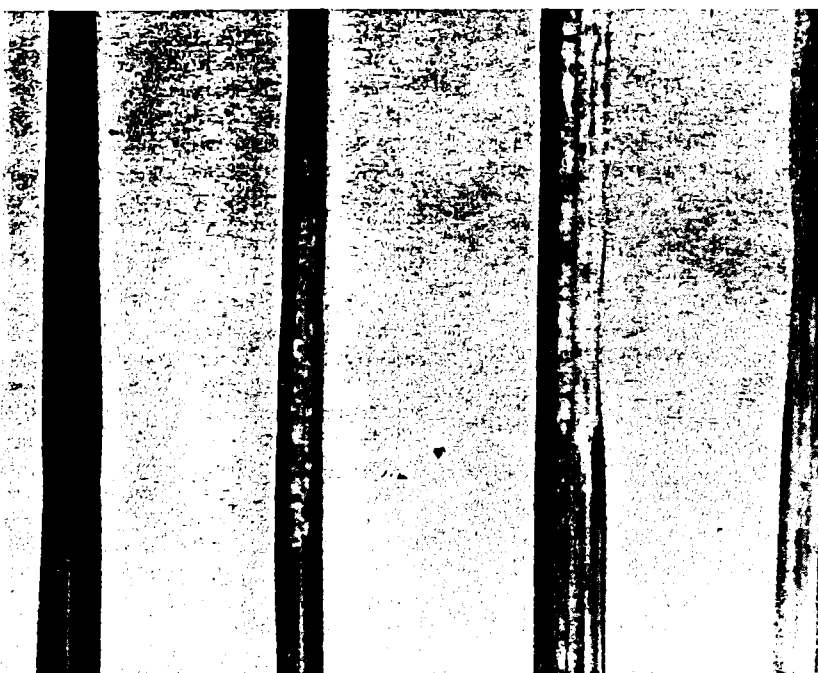


FIG. 1.—Symptoms of damage by *P. bicornis* on Coastal bermudagrass leaves. Leaves from left to right show: (1) normal, disease-free; (2) stippled; (3) streaked; and (4) brown or dead. Approximately $\times 3$.



FIG. 2.—Cross section of leaf bundle above area of visible symptoms. Arrow points to damaged parenchymal cell adjacent to xylem. $\times 100$.

sheaths removed), developed leaf symptoms above and below the point of confinement. Forked plants on which adults had been confined for 24 hr on a 1-in. length of stem (leaf sheaths removed) above the fork developed leaf symptoms above and below the point of feeding but not on the other arm of the fork.

Cross sections of leaves above areas with macroscopic stippling showed slight damage. In many instances, 1 or 2 cells of the border parenchyma adjacent to xylem elements were discolored, and a slight chlorophyll reduction was evident in the adjacent mesophyll (Fig. 2). A cross section through the stippled areas showed that the cell walls of the border parenchyma around many of the vascular bundles were brown and the border parenchyma cells were void of chlorophyll. Most mesophyll in the vicinity of the damaged border parenchyma was also void of chlorophyll. The chlorophyll content of mesophyll cells increased with distance away from the affected vascular bundles. Cross sections of leaves showing severe stippling and streaking revealed collapsed border parenchymal and mesophyll cells around most vascular bundles with only very little chlorophyll remaining in isolated cells (Fig. 3).

Cross sections of stems above and below feeding points of both adults and nymphs had randomly distributed discolored vascular bundles. In many instances, both phloem and xylem were collapsed. Since these observations were not made from serial sections, the relationship of discolored bundles to points of feeding was not established. Cross sections of stems through numerous feeding tunnels made by nymphs and adults, revealed no differences in the type of tun-

nel; both nymphs and adults probe into the xylem. In some instances the probe extended through 1 vascular bundle on into the xylem element of a deeper or adjacent vascular bundle. In several cases the feeding tunnel was forked, with each arm of the fork ending in the xylem element of separate vascular bundles (Fig. 4). Feeding tunnels varied from 30–45 μ in width. New feeding tunnels were not discolored, whereas older feeding tunnels were bordered by brown dead cells, and the vascular bundles into which the insect probed were also brown.

DISCUSSION AND CONCLUSIONS

The most striking result of these experiments was that the nymphs failed to cause any macroscopic symptoms on Coastal bermudagrass, even though they were allowed to feed on the same plants continuously from the age of 4–7 days until they emerged as adults some 35–60 days later, whereas the newly emerged adults often caused symptoms after being confined to a pot of Coastal bermudagrass for only 1 hr. Beck (1963) reported some damage from nymphs. However, since the newly emerged adults can cause symptoms by feeding for no longer than 1 hr, it is plausible that in his tests some nymphs may have matured and fed before they were removed. The habit of feeding could not be used as an explanation for the failure of nymphs to produce symptoms because both nymphs and adults feed in the xylem, and cross sections of their respective feeding tunnels were identical under microscopic examination.

The stippling and streaking observed during these



FIG. 3.—Cross section of leaf bundle in the area of visible symptoms. $\times 100$.

tests had not been observed by us previously or, insofar as we can ascertain, reported in the literature. However, after observing the stippling and streaking in the greenhouse, we have found them in abundance in the field. Perhaps these symptoms were overlooked in the past because no one suspected such manifestations to be a part of the symptom complex caused by the two-lined spittlebug.

Our experiments, which were designed to determine if the damage to Coastal bermudagrass is caused by feeding of a toxicogenic insect or whether the insects serve only as vectors for pathogenic organisms (such as a virus), wholly support our theory that the damage results from the feeding of a toxicogenic insect. After removal of the insects, the damaged plants always recovered and new growth appeared normal in every respect. The severity of damage was related to length of feeding time and degree of infestation. The insects were capable of producing damage even though they had been reared on disease-free Coastal bermudagrass, pearl millet, oats, St. Augustinegrass, and centipedegrasses.

The only possibility that could not be excluded in these tests is that the damage might be caused by a virus transmitted through the egg, but which the insect was not able to transmit until it became an adult. However, if this were a virus, it would have to be one which causes severe initial symptoms and then,

in the absence of the insects, permits the plant to return to normal and thereafter serve only as a symptomless carrier. Such is not the case, because other experiments we have conducted here at Tifton have indicated that when new insects are placed on recovered plants, typical symptoms reappear. Also our arguments are in substantial agreement with those proposed by Carter (1939, 1962) and Leach (1940) in differentiating phytotoxemia from a virus, and parallel those of Williams (1921) and Withycombe (1926), who concluded that sugarcane blight is a disease caused by a toxicogenic spittlebug, *Aeneolamia varia saccharina* Distant. Therefore, we conclude that *P. bicincta* causes phytotoxemia of Coastal bermudagrass.

Confining the spittlebug to various portions of the stem demonstrated that the toxic principle is translocated in the plant. Since symptoms appear in the leaves both above and below the points of feeding, it is evident that the toxin moves both up and down the stem.

Histological studies indicated that the toxic substance moves in the xylem. Feeding tunnels always ended in xylem elements. Cross sections of leaf tissue above macroscopically visible stippled areas, showed that cells of border parenchyma adjacent to xylem elements must be damaged before the adjacent mesophyll tissue showed any effects from the toxin. In the stippled areas, the damage to border parenchyma was more severe than to the adjacent mesophyll, and the damage became less as the distance from the vascular bundles increased. Cross sections of stems indicated that the sclerenchymous sheaths surrounding the vascular bundles were impervious to the toxin, thus forcing it to move into the leaves before "breaking out" through the more pervious parenchymous sheaths. Some discoloration occurred along the sides of the feeding tunnels, possibly a reaction to wounding rather than an effect of a toxin.

Since symptoms resulted only from adult feeding, the nymph apparently does not produce the toxin, or if it does, it is produced in such small quantities that no visible symptoms develop on the plant.

In these studies, the first indication of damage to both parenchymal and mesophyll cells was the loss of chlorophyll, an indication that the toxin may break down chlorophyll or interfere with chlorophyll synthesis. Since both border parenchymal and mesophyll cells were also killed, it is evident that the toxin interferes with additional vital functions in cell metabolism. It is interesting to note that the tops of Coastal bermudagrass plants could be completely killed by the toxin and new growth would be initiated from below ground. Future studies should be designed to determine if the toxin fails to be translocated below the ground in the same quantities as above ground, or if sclerenchymous tissue prevents it from entering into the various tissues in the roots and rhizomes.

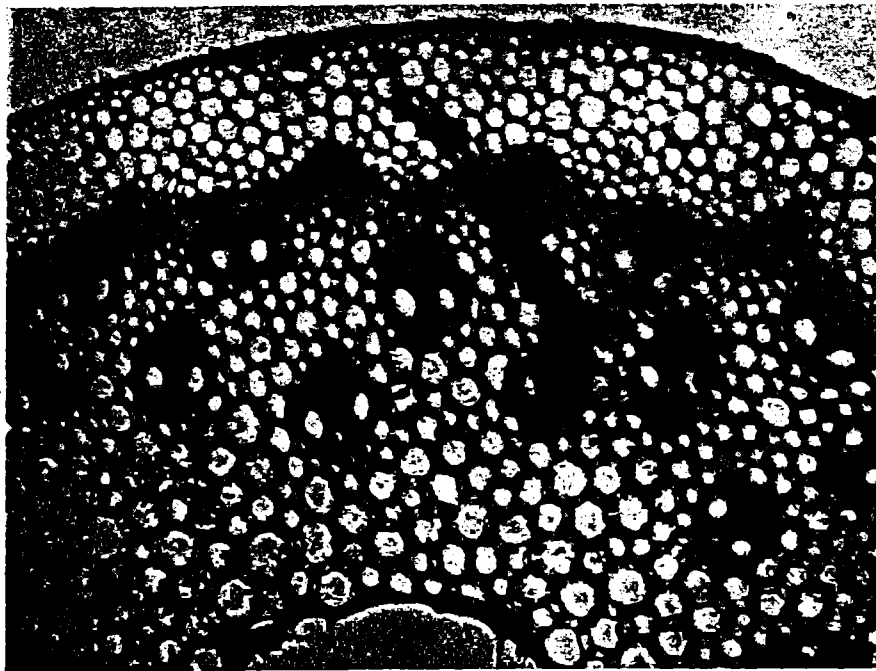


FIG. 4.—Cross section of Coastal bermudagrass stem, showing the adult feeding tunnel of *P. bicincta* ending in the xylem. $\times 100$.

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Reprinted from the
ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA
Volume 59, Number 6, pp. 1067-1071, November 1966

An Improved Methodology for Massive Screening of *Brachiaria* spp. Genotypes for Resistance to *Aeneolamia varia* (Homoptera: Cercopidae)

CESAR CARDONA, JOHN W. MILES, AND GUILLERMO SOTELO¹

J. Econ. Entomol. 92(2): 490-496 (1999)

ABSTRACT Several species and genera of spittlebugs (Homoptera: Cercopidae) are economic pests of grasses in tropical America. They have the potential to cause serious losses on millions of hectares of improved pastures based on cultivars of several species of *Brachiaria*. Most of the available commercial cultivars of *Brachiaria* are susceptible to spittlebug. Resistance has been identified in several germplasm accessions and in one of the commercial cultivars, *B. brizantha* (A. Rich.) Stapf 'Marandú'. *Brachiaria* breeding projects require reliable techniques to screen for host plant resistance in large, segregating populations. A series of experiments was conducted to improve evaluation methodology. A smaller plant growth unit, supporting a single-stem, vegetative propagule, was developed and tested. Infestation levels for both adults (6 per plant) and for nymphs (10 per plant) were established. The refinements in screening methodology increase both reliability and capacity of the screen. Infestation of smaller plant propagules saves time, space, and physical resources. It also allows clear expression of insect damage symptoms and hence permits discrimination between tolerance and antibiosis in host plant reaction. Selection can be based on both resistance mechanisms. We outline a 2-yr *Brachiaria* breeding cycle which incorporates the new spittlebug resistance screening methodology.

KEY WORDS *Aeneolamia varia*, *Brachiaria* spp., resistance, mechanisms, antibiosis

A NUMBER OF grasses in the genus *Brachiaria* (Trin.) Griseb. have become important in tropical America as forages, particularly on infertile soils. The most widely grown are *B. decumbens* Stapf ('Basilisk'), *B. humidicola* (Rendle) Schweick ('Tully' and 'Llanero'), and *B. brizantha* (A. Rich.) Stapf ('Marandú') (Keller-Grein et al. 1996). Existing commercial cultivars are natural polyploid apomicts, thus each is a single genotype (Valle and Savidan 1996). With the exception of Marandú, commercial *Brachiaria* spp. genotypes are very susceptible to several spittlebug species comprising 8 genera (Ferrufino and Lapointe 1989, Lapointe et al. 1992). *Aeneolamia varia* (F.) is one of the most common species (Valério et al. 1996). Both nymphs and adults of this and other spittlebug species cause severe damage. As a result, the entire above-ground portion of the plant appears dry and dead. Dry matter production is reduced and forage quality is affected, thus reducing the productivity of damaged pastures (Valério et al. 1996). Although the economic impact of spittlebug damage has not been properly assessed, it is widely recognized that spittlebug susceptibility is among the most important constraints limiting the use of improved pastures in well-drained, acid soil savannas of tropical America (Lapointe et al. 1992, Miles and Valle 1996).

Host plant resistance to spittlebug may be the only sustainable method of control for an insect that attacks grasses throughout millions of hectares. High levels of antibiosis resistance to *A. varia* have been detected in a number of *Brachiaria* accessions (Nilakhe 1987, Ferrufino and Lapointe 1989, Lapointe et al. 1989a). *Brachiaria* breeding programs were initiated in CIAT (Colombia) and EMBRAPA (Brazil) in the late 1980s. These were based on a sexual tetraploid developed in Belgium from the natural diploid sexual *B. ruziziensis* Germain & Evrard. This sexual tetraploid biotype allowed genetic recombination between the closely related tetraploid apomictic species *B. decumbens* and *B. brizantha* (Swenne et al. 1981). The broad objective of the breeding projects is to combine the edaphic adaptation and quality characteristics of *B. decumbens* with the spittlebug resistance of *B. brizantha* Marandú in productive, high quality, apomictic genotypes (Lapointe and Miles 1992, Miles et al. 1995, Miles and do Valle 1996).

Because of the notoriously erratic spatial and temporal distribution of spittlebugs in naturally infested field plots (Ferrufino and Lapointe 1989), a bioassay designed to detect antibiosis, but not tolerance, was developed. This bioassay, based on artificial infestation of large plants grown in pots (20.3 cm diameter) in the glasshouse, was developed by Lapointe and collaborators (Ferrufino and Lapointe 1989, Lapointe et al. 1992). This assay involves establishing a constant number of nymphs per plant by infestation with eggs.

¹Centro Internacional de Agricultura Tropical, CIAT, Apartado Aéreo 6713, Cali, Colombia.

Resistance (antibiosis) is assessed as percentage survival of nymphs to adult stage. This bioassay, referred to here as the traditional method, has the advantage over naturally infested field plots of greatly improved reliability and precision. With artificial mass rearing of the insect, evaluation of resistance is independent of environmental conditions in the field. However, the traditional method is costly, both in terms of physical resources (pots, soil, and glasshouse space) and in the technical manpower required to recover and count emerging adults over a period of nearly 1 mo. Because of the large size of the infested plants relative to the level of infestation, assessment of symptoms of plant damage from insect feeding is unreliable with this methodology.

The overall objective of the series of experiments reported here was to develop and evaluate a cheaper, quicker, and more reliable method of screening for resistance to spittlebug. In particular, we evaluated a much smaller plant growth unit, supporting a single-stemmed, rooted cutting rather than a multistemmed plant. We sought to determine optimum levels of infestation with both adults and nymphs which allow reliable discrimination between susceptible and resistant genotypes while being logistically feasible. To identify different mechanisms of host plant resistance to spittlebug in *Brachiaria*, we compared the reactions of a common set of host genotypes to artificial infestation with adults or with nymphs, as well as the effect of these same genotypes on nymphal survival. Further, we present data demonstrating the value of evaluating plant damage from nymphal feeding, an aspect that, in spite of its importance (Byers and Wells 1966, Hewitt 1989), has been neglected by other authors (Nilakhe 1987, Valério and Nakano 1992).

Materials and Methods

Plant Materials and Insects. Based on previous studies (Lapointe et al. 1992) germplasm accessions CIAT 0606 (*B. decumbens* Basilisk, susceptible), CIAT 0654 (common *B. ruziziensis*, susceptible) and CIAT 6294 (*B. brizantha* Marandú, resistant) were used as controls in screening trials. These genotypes were originally obtained from CIAT's Germplasm Unit. For all experiments reported here, vegetative propagation by cuttings was used to produce host plants. CIAT 0654 and CIAT 6294 also were used to determine optimum levels of infestation with adults and with nymphs. Thirty-six hybrid-derived clones of known reaction to spittlebug were used to compare the traditional (Ferrufino and Lapointe 1989) and the improved screening methods.

Aeneolamia varia was used in all experiments. Insects were mass-reared in a screenhouse following the methodology developed by Lapointe et al. (1989b). CIAT 0654 is the susceptible substrate on which the mass rearing facility is maintained. Newly emerged adults and mature eggs obtained by the methods described by Lapointe et al. (1989b) were used in the different experiments.

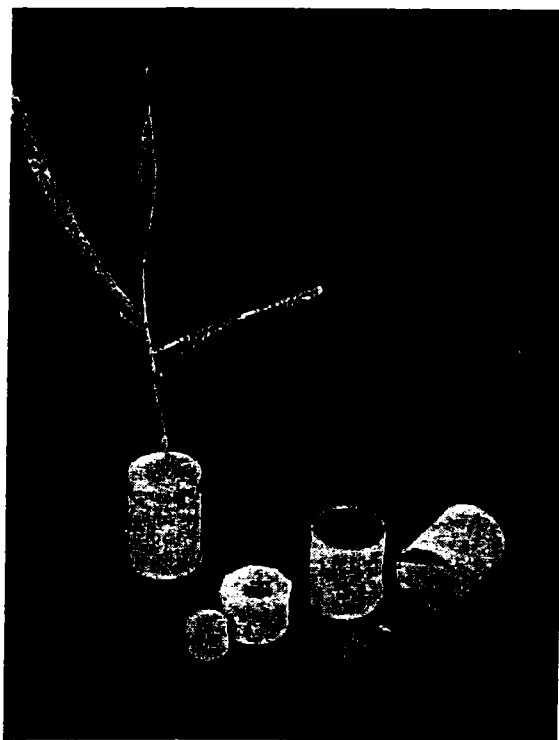


Fig. 1. Plant growth unit used for evaluation of *Brachiaria* genotypes for resistance to spittlebug.

Development of a New Plant Growth Unit for Resistance Evaluation. Several alternatives were compared. The one chosen can be called the single-tube technique. It consists of a PVC tube (5.3 cm diameter, 6.5 cm long), open at both ends, and topped with a cap (4.8 cm diameter, 3.0 cm long) provided with a 2.5-cm central hole through which a single plant stem is placed (Fig. 1). A plastic sheet (5.3 cm diameter) is taped to the lower, open end of the tube to hold soil while allowing excess water to drain. The tube is half-filled with 36 g of sterilized soil (pH 4.8) fertilized with the equivalent of 50 kg/ha each of N, P, and K. This soil forms a layer of ≈ 1.4 cm sustained by the plastic sheet. A single stem cutting is planted and held in place by means of a cylindrical piece of foam rubber inserted in the central opening in the cap. The cap and the foam rubber create a dark, humid environment at the base of the cutting that promotes rooting in the soil substrate. After initial rooting for 2 wk, the entire unit is inverted. With the tube inverted, the plastic sheet disk is removed from the bottom (now the top of the inverted tube), and the 1.4-cm layer of soil, permeated with roots, is pushed toward the top of the tube. The resulting space at the bottom of the tube is filled with soil (≈ 40 g) and the plastic sheet disk replaced. After growing upside down for 1 wk to promote proliferation of superficial roots which will serve as feeding sites for nymphs, the units are returned to an upright position and arranged in shallow trays. They are grown for an additional week in a glasshouse at a mean temperature of 24.2°C (range, 19–27°C) and mean relative

humidity of 75% (range, 70–90%). If propagation is successful, the single-stem rooted cuttings are ready for infestation 1 mo after planting.

Levels of Infestation. *Adults.* To determine optimum levels of infestation for resistance screening using the new plant growth unit, 30-d-old plants (a preliminary trial showed no difference in resistance expression between 15- and 30-d-old plants) of the resistant accession CIAT 6294 and the susceptible accession CIAT 0654 were each infested with 2, 3, 4, 5, 6, 7, 8, 9, or 12 newly emerged adults per plant. An uninfested control was included. For each level of infestation, 10 plants of each genotype were infested inside separate 60-cm, cubical, muslin-covered cages. Hence, the experimental unit was a single cage with one genotype-infestation level combination. The experiment was replicated 3 times in complete blocks in time. The genotype-infestation level treatment combinations were randomized among cages within blocks. Damage scores were recorded on an individual plant basis. The adults were allowed to feed for 10 d and then removed. The plants were immediately scored for damage symptoms by means of a 1–5 visual scale (1, no visible damage; 2, 25% of foliar area affected; 3, 50%; 4, 75%; 5, all foliar area affected and dry). The plants were cut at soil level, taken to a laboratory and dried in an oven at 40°C. Dry weight of plants at each infestation level was then recorded and the data were used to calculate percentage dry weight losses with respect to corresponding uninfested controls.

Nymphs. To determine optimum levels of infestation with nymphs, 30-d-old plants of CIAT 6294 and CIAT 0654 were exposed to 2, 3, 5, 7, 10, 12, or 15 nymphs per plant. Uninfested controls were used for comparison. In a completely randomized design with 10 replications (single-plant experimental unit), each single-plant growing unit was infested with mature eggs of *A. varia* previously selected for viability by visual inspection and incubated in the laboratory (Lapointe et al. 1992). Eggs were checked 24 h after infestation and unhatched eggs were replaced. Most often, selection of eggs in the laboratory translates into 100% eclosion. Infestation was allowed to proceed without interference until all nymphs were fully mature or adult emergence first occurred. At this point, plants were scored for symptoms using the same scale as for adult damage. The experiment with nymph infestation was repeated.

Comparison of Screening Methodologies. To determine the reliability of the new screening technique to detect resistance and to characterize further the mechanisms underlying resistance to spittlebug, 39 genotypes were chosen. These included the germ-plasm accessions CIAT 0606, CIAT 0654, and CIAT 6294 plus 36 hybrid clones previously evaluated for reaction to spittlebug by the traditional methodology (Ferrufino and Lapointe 1989, Lapointe et al. 1992). The 39 genotypes were propagated to single-plant PVC growing units as previously described. Two sets of 10 plants each were propagated for each genotype. Two experiments were conducted. Each consisted of 10 replicates of single-plant experimental units in a

completely randomized design. One experiment was infested with adults, the other with nymphs. To infest with adults, 390 (10 reps, 39 genotypes) 30-d-old plants were placed inside a muslin-covered cage (2 m long, 0.8 m wide, 1 m tall). The level of infestation was 6 adults per plant. Adults were allowed to feed for 10 d and then removed. The plants were immediately scored for damage symptoms by means of the 1–5 visual scale previously described. Genotypes were arbitrarily classified as resistant, intermediate, or susceptible on the basis of mean score as follows: 1–2, resistant; 2.1–3.0, intermediate; >3.0, susceptible.

To evaluate resistance to nymphs, 30-d-old plants were infested with 10 mature eggs previously selected and incubated in the laboratory (Ferrufino and Lapointe 1989). Eggs were checked 24 h after infestation, and unhatched eggs were replaced. Nymphal development was allowed to proceed without interference until full maturity or adult emergence first occurred. At this point, plants were scored for symptoms using the above mentioned scale and genotypes were classified as resistant, intermediate, or susceptible as explained previously. In addition, the number of live nymphs and/or adults present in each pot was recorded to calculate percentage nymph survival which was then used to classify the genotypes as resistant (<30% survival), intermediate (31–50%), and susceptible (>50%). Resistance ratings for each genotype were compared with those obtained in previous years using the traditional screening methodology.

Statistical Analysis. All data were submitted to statistical analysis using SAS (SAS Institute 1988). Regressions of visual damage scores (means of 10 single-plant observations per experimental unit, 3 replicates) and percentage dry weight reduction (2 replicates only) on adult infestation levels were analyzed separately for each replicate and genotype. Data from the uninfested, control treatments were excluded from the regression analysis. Intercepts were compared and regression coefficients were tested for homogeneity. Similarly, regressions of visual damage scores on nymph infestation levels (single-plant experimental units, 10 replicates per experiment) were calculated for each of the genotypes in 2 experiments and then tested for homogeneity of intercepts and regression coefficients. In the trials aimed at comparing the traditional with the new screening methodologies, data were analyzed by 1-way analysis of variance (ANOVA). Descriptive statistics and simple linear correlation coefficients between response variables also were determined using SAS (SAS Institute 1988). When the *F* test was significant, comparison of means was by the least significant difference (LSD) test ($P < 0.01$). Percentages were transformed to arcsine $\sqrt{\text{proportion}}$. Untransformed means are presented.

Results and Discussion

Levels of Infestation with Adults and Nymphs. Analyses of the regression of mean damage scores on adult infestation levels for the 3 replications separately

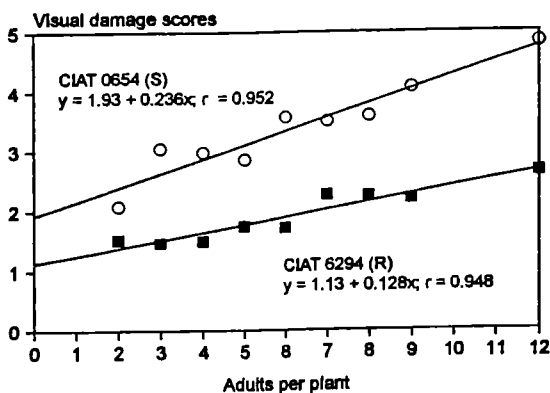


Fig. 2. Relationship between adult infestation levels and damage (assessed using a 1–5 visual scale) caused by *A. varia* on 2 *Brachiaria* spp. genotypes.

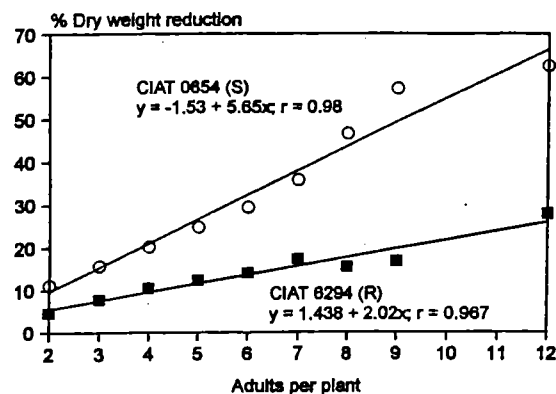


Fig. 3. Relationship between adult infestation levels and percentage dry weight reduction caused by *A. varia* on 2 *Brachiaria* spp. genotypes.

gave no evidence either of differences in intercepts or of nonhomogeneity of the 3 regression coefficient estimates for either the susceptible (CIAT 0654; $F = 0.92$; $df = 2, 21$), or the resistant (CIAT 6294; $F = 1.13$; $df = 2, 21$) genotype. Hence, data from the 3 replicates were pooled and a single regression (Fig. 2) was calculated for each genotype (using means over replicates). Susceptible and resistant genotypes differed in response to increasing levels of infestation ($t = 2.62$, $df = 14$ ($\alpha = 0.05$)). As shown in Fig. 2, the relationship between adult infestation levels and visual damage scores for the susceptible genotype CIAT 0654 can be expressed as $y = 1.93 + 0.236x$, where x is the number of adults per plant (SE of regression = 0.029; $r = 0.95$). According to this relationship, damage levels of 3.1 and 3.5 (susceptible reactions) are obtained with levels of infestation of 4.9 and 6.6 adults per plant, respectively. A level of infestation of 6 adults per plant was chosen for future routine screening.

We observed less damage on CIAT 6294 than on a susceptible host genotype (CIAT 0654) at a given level of adult infestation. Increasing the level of adult infestation produced a smaller reduction in host plant dry weight on CIAT 6294 than on CIAT 0654 ($t = 14.3$, $df = 14$, $P < 0.001$) (Fig. 3). The low level of adult damage on CIAT 6294 may be a reflection of either of 2 distinct mechanisms (or a combination of both), which are impossible to distinguish with the experimental procedure used in the current study. Tolerance to adult spittlebug of CIAT 6294 and a few other *Brachiaria* spp. genotypes, expressed as number of insect-days required to cause severe feeding damage in fully grown plants, was reported by Ferrufino and Lapointe (1989). However, a lower level of damage at a given level of infestation may be a result of reduced feeding rather than true tolerance. Lapointe et al. (1992) assessed adult feeding by measuring 24-h production of excreta of adults confined in Parafilm sachets to plants of different *Brachiaria* genotypes. Their data show that excreta production (hence, feeding) was less on CIAT 6294 than on a susceptible (CIAT 0606) or on a tolerant host (CIAT 6133, *B. humidicola*

Llanero), a result that they suggest may be caused by a toxin or antifeedant in CIAT 6294. Hence, reduced feeding rather than true tolerance may explain the low level of adult damage symptoms and the lower rate of dry weight reduction with increasing infestation levels found here for CIAT 6294. Whatever the cause, our results confirm that this effect can be measured by means of a simple bioassay in only 10 d. Visual damage scores proved to be efficient in predicting biomass losses as demonstrated by the close relationship between visual damage score and percentage dry weight reduction ($r = 0.944$, $P < 0.001$).

Regressions of mean visual damage scores on nymph infestation levels for the susceptible genotype CIAT 0654 in 2 consecutive trials did not differ in terms of intercepts ($F = 0.98$; $df = 1, 18$; $P < 0.01$) or slopes ($t = 0.12$, $df = 10$, $P < 0.01$). The single regression line calculated (Fig. 4) indicated that the relationship between nymph infestation levels and visual damage scores can be expressed as $y = 2.10 + 0.167x$, where x is the number of nymphs per plant (SE of regression = 0.009; $r = 0.992$). According to this,

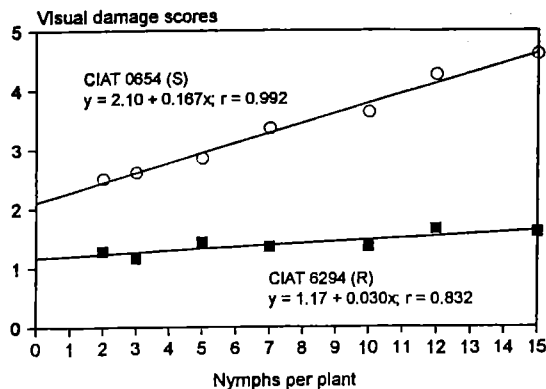


Fig. 4. Relationship between nymph infestation levels and damage (assessed using a 1–5 visual scale) caused by *A. varia* on 2 *Brachiaria* spp. genotypes.

damage levels of 3.1 and 3.5 (susceptible reactions) are obtained with levels of infestation of 6 and 8.4 nymphs per plant, respectively. Fully susceptible reactions (4.0) would be obtained with 11.3 nymphs per plant. We decided to set the level of infestation for future screenings at 10 nymphs per plant. This facilitates handling of the material by technical support staff and calculations of percentage survival based on 10 nymphs per replication, 10 replications per genotype, in large-scale screenings for resistance. A single regression line also was calculated for the resistant genotype CIAT 6294. The relationship can be expressed as $y = 1.17 + 0.03x$ (SE of regression = 0.009; $r = 0.832$). The minor damage shown by CIAT 6294 at high infestation levels is an expression of the antibiotic effect present in this genotype (Ferrufino and Lapointe 1989, Lapointe et al. 1992). Regression analysis showed that the 2 lines in Fig. 4 have significantly different slopes ($t = 2.44$, $df = 10$, $P < 0.05$). This difference suggests that evaluation of genotypes for nymphal damage scores 30–35 d after infestation could be used to discard susceptible genotypes that lack antibiosis or tolerance to nymphal damage. The ones showing little damage would be checked for nymphal survival to ascertain that they do possess antibiosis. This ability to screen for both tolerance and antibiosis is an important advance in the massive screening of genotypes. Previous screening methodologies based selection on percentage survival of nymphs feeding on fully grown plants, which made evaluations of nymphal damage slow, difficult, and unreliable.

Comparison of Screening Methodologies. One-way ANOVA for the 39 genotypes used to compare screening methodologies revealed highly significant differences among genotypes tested for adult damage scores ($F = 11.43$; $df = 38, 347$; $P < 0.0001$), nymphal damage scores ($F = 11.87$; $df = 38, 339$; $P < 0.0001$), and for percentage nymphal survival ($F = 2.57$, $df = 38, 339$; $P < 0.0001$). Mean adult damage scores ranged from very low (1.6) to very high (4.8, plant death); mean nymphal damage scores from 1.6 to 5.0 (plant death). Mean percentage survival ranged from 18 to 77. Adult damage score and percentage nymphal survival were not correlated ($r = 0.152$, ns; ($\alpha = 0.05$), suggesting independence of resistance mechanisms. Nymphal damage score and percentage survival were correlated ($r = 0.552$, $P < 0.01$).

Concurrent testing of the same 39 genotypes for adult and for nymph attack, with rigorous selection for resistance, allowed classification of the genotypes according to different mechanisms of resistance. In Fig. 5, genotypes occupying the lower left quadrant (the hybrids BR 93NO/1371, FM 9406/1044/025, and BRCRUC 1027-0110, and the resistant control CIAT 6294) would be selected for having a low level of adult damage combined with antibiotic resistance to nymphs. Genotypes falling in the upper left quadrant may have tolerance to adult damage but would not be selected because previous release of cultivars expressing tolerance to spittlebug has led to breakdown of resistance under high insect pressure (Lapointe et al.

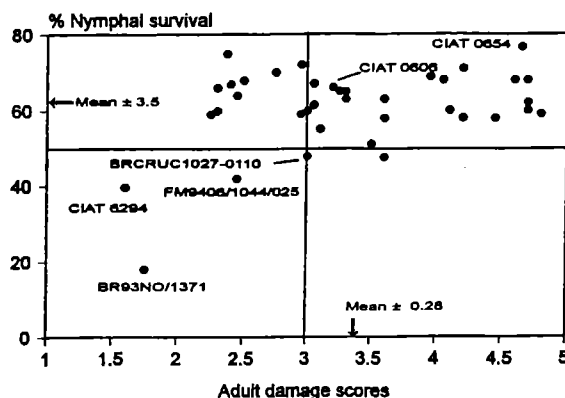


Fig. 5. Relationship between adult damage scores and percentage survival of nymphs in 39 *Brachiaria* spp. genotypes evaluated for resistance to the spittlebug *A. varia*. CIAT 6294 is the resistant control; CIAT 0606 and 0654 are susceptible controls. Solid lines mark cut-off points for resistance (≤ 3.0 for visual damage scores, $\leq 50\%$ for nymphal survival).

1992). All other genotypes (right-hand quadrants, Fig. 5) were susceptible. However, graphic representation of nymphal damage scores and percentage nymphal survival (Fig. 6) revealed that only 3 of the genotypes (lower left quadrant) were truly resistant. These are the hybrids BR93NO/1371 and BRCRUC 1027-0110 and the resistant control, CIAT 6294. The hybrid FM 9406/1044/025 is not truly antibiotic. Its low level of nymphal survival was caused by depletion of food substrate (as reflected by the high nymphal damage score) rather than to antibiosis. Interestingly, none of the genotypes tested exhibited tolerance to nymphal attack (i.e., high survival but low nymphal damage). The other genotypes depicted in Fig. 6 were classified as susceptible.

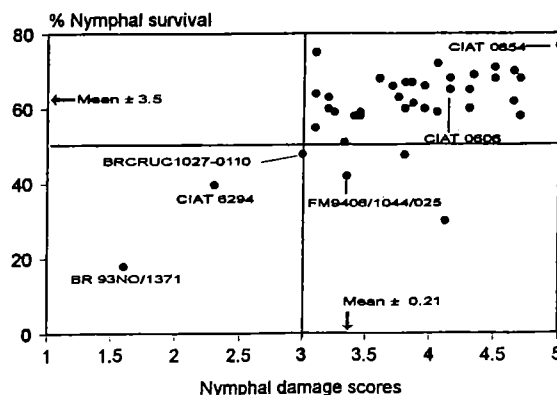


Fig. 6. Relationship between nymphal damage scores and percentage survival of nymphs in 39 *Brachiaria* spp. genotypes evaluated for resistance to the spittlebug *A. varia*. CIAT 6294 is the resistant control; CIAT 0606 and 0654 are susceptible controls. Solid lines mark cut-off points for resistance (≤ 3.0 for visual damage scores, $\leq 50\%$ for nymphal survival).

Table 1. Resistance to *A. varia* in selected *Brachiaria* spp. genotypes

Genotype	Adult damage scores ^a	Nymph damage scores ^a	% nymph survival
BR 93NO/1371	1.7 ± 0.23c	1.6 ± 0.12e	18.0 ± 5.5d
BRCRUC 1027-0110	3.0 ± 0.48b	3.0 ± 0.19c	48.0 ± 7.5bc
CIAT 6294 ^b	1.6 ± 0.19c	2.3 ± 0.21d	39.7 ± 6.5c
CIAT 0606 ^c	3.2 ± 0.30b	4.3 ± 0.18b	65.0 ± 7.8ab
CIAT 0654 ^c	4.6 ± 0.18a	5.0 ± 0.0a	76.7 ± 5.5a

^a On a 1–5 scale (1, no damage; 5, dead plant). See text for details.

^b Resistant control.

^c Susceptible control.

Means ± SEM of 10 replications per genotype. Means within a column followed by the same letter are not significantly different by LSD ($P < 0.01$).

The difficulties in handling large numbers of adults, and the fact that adult damage scores can be misleading, led us to conclude that mass screening of genotypes for a plant breeding program must be conducted using infestation with nymphs. With the new screening technique it is possible to select for nymphal damage scores first, discard genotypes showing high damage scores, then count surviving nymphs (a lengthy, tedious process) only on those with low damage scores. Bioassays of selected genotypes with adults can be used later to detect tolerance, a mechanism that is a useful component of spittlebug resistance only when coupled with antibiosis (Ferrufino and Lapointe 1989, Miles et al. 1995).

Levels of resistance in selected genotypes are shown in Table 1. As compared with the susceptible controls CIAT 0606 and CIAT 0654, the hybrid BR93NO/1371 was outstanding, combining low adult damage and antibiosis to nymphs. This genotype was classified as highly resistant. In fact, it is the most resistant *Brachiaria* genotype tested to date for resistance to *A. varia*. The resistant control, CIAT 6294 (Marandú), expressed a low level of adult damage and showed low nymphal damage but was intermediate for nymphal survival. The hybrid BRCRUC 1027-0110 was classified as intermediate. Results obtained with CIAT 6294 and with the susceptible accessions CIAT 0606 and CIAT 0654 were consistent with those obtained in previous years by Ferrufino and Lapointe (1989) and Lapointe et al. (1992). Resistance ratings obtained with the new screening technique were compared with those obtained using the traditional methodology in previous years. As shown in Table 2, all genotypes found to be susceptible by the traditional methodology also were susceptible by all criteria using the new methods; of those rated resistant using the traditional screening method, 1 (BRCRUC 1016-0009) was susceptible on nymphal survival and 2 were classified as intermediate, suggesting that the new technique may be more stringent in characterizing antibiosis. BR93NO/1371 was highly resistant by all criteria. We conclude that the glasshouse screening methodology developed as a result of this work is reliable and consistent for selection of *Brachiaria* spp. genotypes with resistance to spittlebug.

Table 2. Comparison of resistance ratings for 39 *Brachiaria* genotypes tested for resistance to *A. varia* using 2 different screening methodologies

Genotypes	According to traditional screening methodology ^a	According to improved screening methodology	
		Nymph damage scores	% nymph survival
BR93NO/1371	R	R	R
CIAT 6294 ^b	R	R	I
BRCRUC 1027-0110	R	R	I
BRCRUC 1016-0009	R	I	S
Four hybrids	I	S	S
29 hybrids	S	S	S
CIAT 0606 ^c	S	S	S
CIAT 0654 ^c	S	S	S

^a Based on percentage nymph survival (Ferrufino and Lapointe 1989, Lapointe et al. 1992). R, resistant; I, intermediate; S, susceptible.

^b Resistant control.

^c Susceptible control.

The new methodology for assessment of reaction to spittlebug represents a major advance in the development of resistant *Brachiaria* cultivars, whether from germplasm accessions or, particularly, in plant breeding programs. The capacity of the new methodology, as measured by genotypes evaluated per unit time, is at least an order of magnitude greater than the former methods, owing to a combination of lower requirements for inputs of materials, labor, and time (70% less space, 70–80% fewer resources, 50% less time). Improved precision means that fewer replications are required, increasing even more the throughput capacity. Although the former methods were adequate and extremely useful in screening a finite collection of germplasm accessions to identify useful sources of resistance, the massive generation of genetic recombinants from the breeding program and time constraints in advancing breeding cycles meant that early generations following initial cycles of hybridization at CIAT were advanced largely in the absence of reliable information on spittlebug reaction.

The two-year breeding cycle in CIAT's *Brachiaria* improvement program is now as follows. Several thousand individual progeny seedlings are produced from open pollination of selected parentals from the previous generation. These are propagated and transplanted to field trials. During the 1st year, ~80% of clones are culled on visual assessment in field trials to leave ~500–1000 genotypes. Early in the 2nd year, these clones are tested in 2 stages for spittlebug resistance with artificial infestation in the glasshouse. First, culling is on nymphal damage, using only 2 replications. The best genotypes (on the order of 100), are then rigorously retested using 10 replicates. Nymphal survival as well as damage are assessed to detect cases of mere tolerance. The 2-stage evaluation of spittlebug resistance can be completed in 4 mo. On the order of 20–50 genotypes selected for spittlebug resistance (and for 2nd-season field performance) serve as parentals for the subsequent breeding cycle. These are then recombined by open pollination of pot-grown plants during the 2nd half of year 2 to complete the cycle.

Although the new methodology is a major advance, still greater capacity would be desirable. Ideally, all of the several thousand open-pollinated progenies produced in each breeding cycle by recombination among parental selections would be evaluated under controlled conditions and with artificial infestation. A major breakthrough along these lines likely will not come until we have developed methodology to achieve reliable infestation of plants in large field trials. This methodology has so far proved elusive because of the multitude of uncontrollable factors operating in the field. Research is in progress to develop methods to deliver the insect to plants in the field under conditions that ensure that effective infestation is consistently achieved.

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Received for publication 20 July 1998; accepted 4 December 1998.

COMUNICAÇÃO CIENTÍFICA

CHARACTERIZATION AND VIRULENCE OF *Metarhizium anisopliae* (METSCH.) SOROK. ISOLATES TO EGGS OF *Deois flavopicta* (STAL) (HOMOPTERA: CERCOPIDAE)

Marcos R. de Faria¹, Myrian S. Tigano¹, Eliana M.G. Fontes¹ e Roberto E. Lecuona²

RESUMO

Caracterização e virulência de isolados de *Metarhizium anisopliae* (Metsch.) Sorok. a ovos de *Deois flavopicta* (Stal) (Homoptera: Cercopidae)

Avaliou-se a variabilidade genética entre 12 isolados de *Metarhizium anisopliae* (Metsch.) Sorok. obtidos de cigarrinhas-das-pastagens, *Deois flavopicta* (Stal) através da análise de isoenzimas, velocidade de germinação dos conídios em meio artificial sólido e virulência ao hospedeiro de origem. Nas análises de isoenzimas não foram detectadas diferenças eletromórficas nos seis sistemas enzimáticos. No entanto, houve variação entre isolados na velocidade de germinação dos conídios e na virulência para *D. flavopicta*. Os valores de tempo de germinação 50% (TG₅₀) variaram de 7:58 a 15:09 (h:min). Os níveis de infecção em ovos na fase de pré-eclosão variaram de 0 a 43,3%. Porém, quando quatro isolados foram testados em ninfas de primeiro instar observou-se 35 a 70% de infecção. Não houve correlação entre as características analisadas.

PALAVRAS-CHAVE: Insecta, cigarrinha-das-pastagens, isoenzimas, controle microbiano, fungo entomopatogênico.

The entomopathogenic fungus *Metarhizium anisopliae* (Metsch.) Sorok. (Deuteromycotina: Hyphomycetes) is considered a promising biological control agent for cercopid insects, including pasture spittlebugs of the genus *Deois* and *Zulia* (Conti *et al.* 1980, Alves 1992). Laboratory and greenhouse bioassays testing this fungus against pasture spittlebugs showed virulence higher than 70% (Araújo & D'Aguar 1975, EMGOPA 1983a, Saldanha *et al.* 1993).

Received 10/21/94. Accepted 10/30/95.

¹EMBRAPA/CENARGEN, Caixa postal 02372, 70849-970, Brasília, DF.

²IMYZA/CICA/INTA, Castelar, Casilla correo 25, 1712 Castelar, Buenos Aires, Argentina.

However, field tests with *M. anisopliae* demonstrated low efficiency, with approximately 5% of infectivity (Ramiro & Cottas 1979, Cottas & Ramiro 1981, EMGOPA 1983b, Carneiro 1988). This low performance is attributed mainly to formulation of the fungus and application methodologies (Alves 1992). Regarding application, there is a poor definition of the timing for introduction of the pathogen, and a lack of information about the more susceptible developmental stages of the host. Phenological and population dynamics studies of the pasture spittlebug *Deois flavopicta* (Stal) indicated that hatching eggs and first instar nymphs of the first generation of this insect, which occur in the beginning of the rainy season each year, would be the best target for the application of entomopathogenic fungi (E.M.G. Fontes *et al.*, not published). In this work we analyzed the virulence of *M. anisopliae* isolates, obtained from adults or nymphs of *D. flavopicta* (Table 1), to hatching eggs of the original host. Some isolates were also tested on first instar nymphs to compare virulence among these developmental stages. Isozyme analysis and conidia germination rate of all isolates were also evaluated in order to understand the relationship between virulence and these two characteristics.

Monoconidial cultures of the isolates were produced and maintained on Sabouraud dextrose agar with yeast extract (40g dextrose, 10g mycological peptone, 10g agar in 1000ml of distilled water, pH 5.6 at 27°C). The conidia were collected after 10 days of cultivation. To determine the germination rate, 50 µl of 10⁶ conidia/ml suspensions were inoculated on Petri

Table 1. Analysis of germination rate of conidia of *Metarhizium anisopliae* obtained from *Deois flavopicta* on artificial medium and virulence to the original host.

Isolates ¹	Geographic origin	Date	TG ₅₀ ² (h:min)	Slope	Mortality(%) ³	
					Eggs	Nymphs
CG 30	Espírito Santo	NI	15:09 a	26.28	3.3	35
CG 31	Rio de Janeiro	NI	12:46 b	17.08	10.0	ND
CG 58	Mato Grosso	1986	12:43 b	17.58	0.0	ND
CG 45	Brasília/DF	1989	12:25 c	8.68	0.0	ND
CG 42	Brasília/DF	1989	11:43 d	11.80	13.3	ND
CG 51	Brasília/DF	1988	11:32 e	5.98	30.0	ND
CG 102	Brasília/DF	1988	11:05 f	5.71	40.0	ND
CG 49	Brasília/DF	1989	10:54 g	4.87	6.7	70
CG 257	Brasília/DF	1988	10:42 h	6.46	3.3	65
CG 54	Brasília/DF	1986	10:39 h	6.76	20.0	ND
CG 112	Brasília/DF	1988	09:04 i	4.82	43.3	55
CG 29	Manaus/AM	NI	07:58 j	9.00	0.0	ND

¹CG = CENARGEN/EMBRAPA Collection, Brasília, DF.

²Time needed for germination of 50% of the conidia on artificial solid medium. Means followed by the same letter do not differ by Duncan's test at 5% level of probability.

³Values are means of three replicates with 10 eggs or 10 first instar nymphs per replicate. No mortality was observed in the controls on the time of evaluation.

NI = not identified.

ND = not determined.

dishes containing the above culture media. A total of 400 conidia (four replicates of 100 conidia) were observed each two hours beginning two hours after inoculation. The data on percentage of germination were used to calculate the TG_{50} (time necessary for germination of 50% of the conidia) using the Probit method. Mycelia needed for biochemical studies were obtained by inoculating 50ml of Sabouraud dextrose broth in 250-ml flasks with a final conidial suspension of 10^6 conidia/ml. Flasks were incubated on a rotary shaker maintained at 150 rpm and 25°C. After seven days, the mycelia were separated from supernatant by filtering through filter paper (Watman # 1). The mycelial mat was then washed several times in SDW and in a 0.05 M Tris-HCL, pH 7.8, buffer to remove residual broth. Mycelia were collected and concentrated by vacuum filtration, weighted, fragmented with liquid nitrogen, and centrifuged at 10.000 g at 4°C for 90 minutes. The supernatant, containing the soluble proteins, was distributed in 1.5 ml tubes and stored at -80°C. The isozymes were separated using isoelectric focusing (IEF) in polyacrylamide gels at 10%, according to the methodology described by Riba *et al.* (1986). Six enzymatic systems were analyzed: alcohol dehydrogenase (ADH), acid phosphatase (ACP), phosphoglucumutase (PGM), glutamate dehydrogenase (GDH), malate dehydrogenase (MDH) and glutamate oxalacetic transaminase (GOT), according to staining procedures adapted from Shaw & Prasad (1970).

Eggs close to hatching and first instar nymphs of *D. flavopicta*, obtained from field collected females, were used on the virulence tests. Eggs were inoculated through topic application of 5 µl of conidia suspension (10^8 conidia/ml) with the aid of a micropipette. Three replicates of 10 eggs were used. After the treatment, the eggs were transferred to Petri dishes covered at the bottom with a thin layer of wet cotton covered with filter paper. This layer was kept permanently wet. Ten rice seedlings were also added to each Petri dishes to feed the nymphs as the egg hatched. The Petri dishes were incubated at 27°C and 12 hours photophase. After 10 days, the percentage of infected eggs was determined by failure of hatching with mycosis and sporulation. The first instar nymphs were immersed for 5 seconds in a suspension containing 10^8 conidia/ml. Three replicates of 10 nymphs were used. After treatment, the nymphs were transferred to Petri dishes, repeating the methodology described above for eggs. After 10 days of the treatment, the percentage of infected nymphs was determined by sporulation of the fungus over the cadaver. Distilled water mixed with Tween 80 at 0.1% was used in the control treatment for both tests.

The enzymatic systems analyzed, although polymorphic for *M. anisopliae* (Riba *et al.* 1986, St. Leger *et al.* 1992), presented homogeneity among *D. flavopicta* isolates used in this study. These results confirm the low variability found among Brazilian isolates of *M. anisopliae* through analysis of isoenzymatic phenotypes (Riba *et al.* 1987, St Leger *et al.* 1992), exoenzymes production (Rosato *et al.* 1981), and pyrolysis-gas chromatography (Messias *et al.* 1983). Using arbitrarily primed analysis PCR, Tigano-Milani *et al.* (1995b) showed high similarity among isolates originally obtained from cercopid insects in Brazil. In the same study, Brazilian isolates obtained from non-cercopid hosts, or from soil, were well separated from the former homogeneous group, probably indicating that the spittlebugs would be acting on the selection of specific genotypes. However, when characteristics better linked to potential of the isolate for biological control agent were analyzed, such as virulence to the original host and germination rate of conidia in artificial media, a high variability among the isolates obtained from the pasture spittlebug, *D. flavopicta*, was observed. The percentage of mortality of *D. flavopicta* eggs caused by *M. anisopliae* varied from 0 to 43%, showing that this stage of development can be susceptible to *M. anisopliae*. First instar nymphs higher susceptibility to *M. anisopliae* than eggs, as the rate of infection varied from 35 to 70% for the four isolates analyzed (Table 1). The isolate CG 49 infected only 6.7% of the eggs, however

the same isolate tested in nymphs showed 70% of infection. Germination of conidia, evaluated through TG_{50} values, varied from 7:59 to 15:09 (h:min) among the isolates studied (Table 1). Although variability was found among the isolates through the analysis of these biological traits, no correlation was observed between virulence and conidial germination. The isolates CG 29 and CG 112 showed capability of fast germination (7:58 and 9:04 h:min, respectively). However, these two isolates showed different behavior in relation to pathogenicity to spittlebug eggs: CG 29 was not pathogenic and CG 112 caused 43.3% mortality (Table 1). The lack of correlation between these parameters was also observed among isolates of another entomopathogenic fungus, *Nomuraea rileyi*, when inoculated on larvae of *Spodoptera frugiperda* (J.E. Smith) (Tigano-Milani et al. 1995a).

These results showed that, for the *M. anisopliae* isolates analyzed, molecular markers such as isoenzymes do not allow separation of isolates based on biological characteristics of interest for biological control. Regarding virulence, eggs of *D. flavopicta* were not so susceptible to *M. anisopliae* as first instar nymphs. Thus, based on the population dynamics of this pest, the selection of isolates virulent to early nymphal stages is indicated, to facilitate the adoption of proper control strategies.

ACKNOWLEDGEMENTS

We thank Bonifácio Magalhães and Edison R. Sujii (CENARGEN/EMBRAPA) for critical review of this manuscript.

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The Biology of Sugar Cane Froghoppers

D. W. FEWKES

*Tate & Lyle Central Agricultural Research Station, Carapichaima, Trinidad**

1. Introduction

Froghoppers or 'spittle bugs' are Homopterous insects of the superfamily Cercopoidea. The classification adopted here is that of Metcalf (1951, 1960, 1961, 1962a, 1962b). Representatives of 14 genera, including 66 species and subspecies, known to feed on sugar cane are listed in Table 1. This list is essentially the same as that of Box (1953), plus a few records due to Guagliumi (1955, 1956, 1962a) and to Fennah (1949, 1951). The nomenclature has been revised after Metcalf (1961, 1962a). Two of the four families recognized by Metcalf are represented (Cercopidae and Aphrophoridae). However, the great majority of sugar cane froghoppers belong to one family, the Cercopidae.

Some species of the genus *Aeneolamia* (Cercopidae) exhibit considerable variation in the shape and depth of colour of the wing markings. This, together with variations in body colour and in the form of the subgenital plates of the males, has led to the recognition of numerous subspecies or ecological races (Guagliumi, 1955). Each subspecies is said to be restricted to the ecological conditions of a particular habitat, within which it is liable to a more or less definable variation.

Although froghoppers are richly represented throughout the tropics and subtropics, they are common pests of sugar cane only in the New World. No froghoppers are recorded from sugar cane in Spain, Egypt, Sudan, East Africa, Mauritius, Réunion, Pakistan, Ceylon, Indonesia, Australia or Hawaii. Practically nothing is known of the biology of the West African (*Locris*, *Poophilus*), South African (*Locris*) and Indo-Burman (*Abidama*, *Callitettix*) sugar cane froghoppers, nor of those from Taiwan (*Poophilus*, *Aphrophora*) and the Philippines (*Poophilus*). This account is therefore mainly concerned with the 9 genera that attack sugar cane in the New World. Most of the species are North, Central or South American. With the exceptions of Trinidad, Tobago and Grenada to the south, and Jamaica and Cuba to the north, froghoppers are not recorded on sugar cane in the West Indian islands.

The most widely distributed genus, and economically the most important, is

* Now at Tate & Lyle Research Centre, Westerham Road, Keston, Kent, England.

TABLE 1

SUGAR CANE FROGHOPPERS (CERCOPOIDEA) OF THE WORLD

Species	Country	Reference
CERCOPOIDAE		
Callitettixinae		
Callitettixini		
<i>Abidama producta</i> (Walk.)	Burma	Shroff (1920)
<i>Callitettix versicolor</i> (F.)	Burma	Shroff (1920)
	India	Butani (1961)
Cercopinae		
Locrisini		
<i>Locris areata</i> (Walk.)	S.Africa (Natal)	van der Merwe (1937)
<i>L. arithmetica</i> (Walk.)	S.Africa (Natal)	van der Merwe (1937)
<i>L. maculata</i> (F.)	Sierra Leone, Gold Coast	Box (1953)
<i>L. vicina</i> Sign.	Madagascar	J. R. Williams (<i>in litt.</i>)
<i>L. sp.</i>	Madagascar	J. R. Williams (<i>in litt.</i>)
Tomaspidini		
<i>Sphenoclypeana parana</i> (Dist.)	Brazil	Moreira (1921)
<i>Tomaspis entreriana</i> Berg	Argentina	Box (1929)
	Brazil	Franco (1953)
<i>T. flavopicta</i> (Stal)	Brazil	Franco (1953)
<i>T. furcata</i> (Germ.)	Brazil	Monte (1932)
<i>T. spectabilis</i> Dist.	Bolivia	Munro (1954)
Cercopini		
<i>Aeneolamia astralis</i> (Dist.)	Argentina	Box (1929)
	Brazil	Franco (1953)
<i>A. flavilatera</i> (Urich)		
<i>A. f. caripensis</i> Fennah	Venezuela	Fennah (1949)
<i>A. f. flavilatera</i> (Urich)	Guyana	Bodkin (1914)
<i>A. f. funebris</i> Fennah	Venezuela	Fennah (1949)
<i>A. f. guarici</i> Guagl.	Venezuela	Guagliumi (1956)
<i>A. f. nirguensis</i> Guagl.	Venezuela	Guagliumi (1962a)
<i>A. f. talmana</i> Fennah	Venezuela	Fennah (1949)
<i>A. lepidior</i> (Fowler)	Panama, Canal Zone	Williams (1921)
	Venezuela	Fennah (1951)
	Brazil	Pestana (1923)
<i>A. postica</i> (Walk.)		
<i>A. p. campecheana</i> Fennah	Mexico (Campeche, Yucatan)	Fennah (1951)
<i>A. p. jugata</i> (Fowler)	Guatemala	Williams (1921)
	British Honduras	Fennah (1951)
<i>A. p. postica</i> (Walk.)	Mexico	Fennah (1951)
<i>A. p. subspp.</i>	Mexico	Box (1953)
<i>A. p. subsp.</i>	El Salvador	Box (1953)
<i>A. reducta</i> (Lallemand)		
<i>A. r. montana</i> Fennah	Venezuela	Fennah (1949)
<i>A. varia</i> (F.)		
<i>A. v. bodkini</i> (Williams)	Guyana	Williams (1921)
	Venezuela	Myers (1932)
<i>A. v. campestris</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. carmodyi</i> (Kershaw)	Tobago	Kershaw (1913a)
<i>A. v. costata</i> Fennah	Venezuela	Fennah (1949)

TABLE 1 (cont.)

Species	Country	Reference
<i>A. v. deltica</i> Guagl.	Venezuela	Guagliumi (1955)
<i>A. v. demissa</i> (Walk.)	Venezuela	Fennah (1949)
<i>A. v. deusta</i> Fennah	Venezuela	Fennah (1951)
<i>A. v. falconiana</i> Guagl.	Venezuela	Guagliumi (1955)
<i>A. v. fallax</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. lugens</i> Fennah	Venezuela	Fennah (1951)
<i>A. v. nigrescens</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. pallidior</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. paspali</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. propinqua</i> (Walk.)	Venezuela	Williams (1921)
<i>A. v. saccharina</i> (Dist.)	Trinidad	Hart (1890)
	Grenada	Hutson (1917)
	Venezuela	Guagliumi (1955)
<i>A. v. sanctaebarbarae</i> Guagl.	Venezuela	Guagliumi (1955)
<i>A. v. semifascia</i> (Walk.)	Venezuela	Fennah (1949)
<i>A. v. sontica</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. sordida</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. tomentosa</i> Fennah	Venezuela	Fennah (1949)
<i>A. v. turenensis</i> Guagl.	Venezuela	Guagliumi (1955)
<i>Delassor murus</i> (China & Myers)	Brazil	Myers (1935a)
<i>D. rubicundus</i> (Walk.)		
<i>D. r. indentatus</i> (Walk.)	Brazil	Monte (1929)
<i>D. tristis</i> (F.)		
<i>D. t. guppyi</i> (Urich)	Trinidad	Pickles (1939)
<i>D. t. monagasi</i> Fennah	Venezuela	Fennah (1949)
<i>D. t. tristis</i> (F.)	Surinam	Williams (1921)
	Brazil	Franco (1953)
<i>Deois morialis</i> (China & Myers)	Brazil	Myers (1935b)
<i>D. knoblauchii</i> (Berg)	Argentina	Box (1929)
	Brazil	Franco (1953)
<i>Monecphora flavifascia</i> Metcalf & Bruner	Cuba	Bruner <i>et al.</i> (1945)
<i>Prosapia bicincta</i> (Say)		
<i>P. b. basalis</i> (Walk.)	Jamaica	Williams (1921)
<i>P. b. bicincta</i> (Say)	Louisiana	Holloway and Loftin (1919)
<i>P. b. fraterna</i> (Uhler)	Cuba	Bruner <i>et al.</i> (1945)
<i>P. b. subsp.</i>	Mexico	Box (1953)
<i>P. simulans</i> (Walk.)	Mexico	Box (1953)
<i>Sphenorhina liturata</i> (Le Pel. & Serv.)		
<i>S. l. ruforivulata</i> (Stal)	Brazil	Dias de Sousa (1951)
<i>S. rubra</i> (L.)		
<i>S. r. sororia</i> (Germ.)	Brazil	Franco (1953)
<i>Cosmoscartini</i>		
<i>Mahanarva indicata</i> Dist.	Brazil	Moreira (1921)
APHROPHORIDAE		
Aphrophorinae		
Ptyelini		
<i>Poophilus adustus</i> (Walk.)	Sierra Leone	Box (1953)
<i>P. costalis</i> (Walk.)	Taiwan	Takano and Yanagihara (1939)
	Philippines	Woodworth (1921)
Aphrophorini		
<i>Aphrophora</i> sp.	Taiwan	Takano and Yanagihara (1939)

Aeneolamia. Froghoppers of this genus are pests of sugar cane in Mexico, Central America, Venezuela, Guyana, Surinam, the islands of Trinidad, Tobago and Grenada, and Brazil and Argentina. The next most important genera are *Mahanarva* (Brazil), *Sphenoclypeana* (Brazil), *Sphenorhina* (Brazil) and *Tomaspis* (Argentina, Bolivia and Brazil). The genera *Delassor* (Brazil, Surinam, Trinidad, Venezuela), *Deois* (Argentina, Brazil), *Monecphora* (Cuba), and *Prosapia* (Louisiana, Mexico, Cuba, Jamaica), are of a relatively minor economic importance in sugar cane.

2. Habitat

The host plants of sugar cane froghoppers include a variety of wild and cultivated grasses, and several sedges (Beck, 1963; Byers, 1965; Golding, 1937, 1940; Guagliumi, 1954, 1962b; Hayward, 1942; Lepage and Monte, 1942; Munro, 1954; Myers, 1932, 1935b; Pickles, 1931a, 1938; Williams, 1921; Wilson *et al.*, 1961). Some species on sugar cane are important pests of pasture grasses. Amongst these are *Aeneolamia lepidior* and *A. reducta montana* in Venezuela (Guagliumi, 1962b), *A. postica postica* and *A. postica campecheana* in Mexico (Caceres and Ruano, 1961), and *Prosapia bicincta bicincta* in the southeastern United States (Beck, 1963; Pass and Reed, 1965). *Prosapia bicincta bicincta* is also recorded from various Dicotyledonous herbs, shrubs and trees in the United States (Byers, 1965).

Since the introduction of sugar cane into the New World in the 16th and 17th centuries, several of the native froghoppers have become adapted to sugar cane plantations as a new environment in which to live, feed and reproduce. Some of them (e.g. *Aeneolamia varia* subsp.) had their original habitat in the grassy clearings of the rain forest (Pickles, 1931a). Others, such as *Aeneolamia postica* subsp. in Mexico, have invaded sugar cane from open pastures (Caceres and Ruano, 1961). The extent of their adaptation to sugar cane varies widely. None of them is restricted to sugar cane, but for some it has become the most usual host plant, whilst others feed on it only occasionally. Thus, in highly adapted species, resident populations are common, whereas less adapted species infest sugar cane as migrants.

There is some evidence that froghoppers are attracted to their preferred host plant by its odour. Fennah (1939) showed that *Aeneolamia varia saccharina* adults are more attracted by the leaf odour of a commercial sugar cane variety, B.H. 10/12, than by that of Guatemala grass (*Tripsacum laxum*) or that of a non-commercial cane (*Saccharum ciliare*). When several sugar cane varieties were planted in the same field, it was found that some sustained more froghopper damage than others (Steven and Potter, 1928; Taylor and Pickles, 1934). However, when planted on a large scale, all commercially grown varieties have, so far, proved

susceptible to attack, although some may have greater powers of recovery than others.

Pickles (1933b) pointed out that plant canes are generally less attacked by froghoppers (*Aeneolamia varia saccharina*) than ratoon canes, partly because resident froghopper populations are largely destroyed by ploughing. In addition, tall cane is generally preferred to short cane, possibly because it offers a more humid and shadier microclimate.

3. Oviposition

Sugar cane froghoppers lay their eggs in the soil and in plant tissue. No species is known to oviposit exclusively in soil, but oviposition of some species is restricted to plant tissue. The site of oviposition seems generally to be related to the location of the young nymphs. Thus, species which feed on sugar cane roots in the nymphal stage (e.g. *Aeneolamia* spp.) lay their eggs mainly in the soil. Pickles (1933b) showed that *Aeneolamia varia saccharina* females lay most of their eggs in soil. A small proportion (1 or 2%) is laid in moist decaying leaf sheaths (cane trash) near the ground. The eggs of *A. flavilatera flavilatera* are also laid almost exclusively in the soil (Pickles, 1945; James, 1946), as are those of *A. postica postica* and *A. postica campecheana* (Caceres and Ruano, 1961). An exception is *Sphenoclypeana parana* which lays its eggs in sugar cane leaves and the nymphs, on hatching, descend to the base of the stools to feed on the roots (Moreira, 1921). The nymphs of *Mahanarva indicata* and *Delassor tristis guppyi* feed in the leaf axils of sugar cane; the eggs of the former species are laid in sugar cane leaves (Moreira, 1921) and those of the latter species are generally inserted into green leaf tissue near the midrib, but may also be laid in moist cane trash or in damp soil (Pickles, 1939).

Oviposition behaviour has been studied in detail for only *Aeneolamia varia saccharina*. When given a choice, froghoppers laid more eggs in acidic clay soils than in black marl (neutral or slightly alkaline) or sandy soils (Hardy and Rodriguez, 1930; Hardy and Urich, 1931a). However, this behaviour was modified by altering the moisture content of the soils. At high moisture levels, the black marl soil became much more attractive for oviposition. The sandy soil, however, was by far the least attractive, whether dry, moist or wet. Hardy and Urich (1931b) showed that, for one particular soil (pH, 7.0; index of texture, 34; sand content, 18%; moisture content at the onset of stickiness, 38%), variations in moisture content determined its attractiveness for oviposition. Some eggs were laid in the soil at each moisture level studied, ranging from 20% to 45%, but most were laid in soil at approximately the onset of stickiness. For *Aeneolamia flavilatera flavilatera*, James (1946) found that females would not oviposit in air dried soil. Eggs were

laid in soils when the moisture content was sufficient to make the soil particles cohere, and in wetter, up to completely saturated, soils.

In the field, oviposition of *A. varia saccharina* is thought to take place at night (Williams, 1921). In laboratory cultures, females also oviposit during the day if kept in a dark place (Urich and Pickles, 1930). Females of *A. flavilatera flavilatera* in laboratory cages would oviposit only in heavy shade or darkness (James, 1946).

The eggs of *A. varia saccharina* are thrust into the cane trash or soil by the short blunt ovipositor of the female, together with a small amount of colleterial secretion (Kershaw, 1913b). They are placed at a slight angle with the anterior end upwards, just projecting from the substrate. In the laboratory, they are readily laid into moist blotting paper (Urich and Pickles, 1930). Although the eggs are laid shallowly in the soil, to a maximum depth of 5/16 in. (Pickles, 1931b), they are commonly found at 1 to 2 in. below the soil surface because females often descend into cracks to lay their eggs (Pickles, 1931c). Females of *A. varia sontica* also lay their eggs in cracks and crevices around the deeper roots (Guagliumi, 1962b).

According to Pickles (1931c), *A. varia saccharina* does not appear to deliberately place its eggs near sugar cane roots. However, there is some evidence that sugar cane roots contain a substance or substances attractive to ovipositing females (Fewkes and Buxo, 1965). Pickles (1933b), studying the distribution of froghopper eggs in cane field soils, found that the eggs were concentrated in and around the cane stools, comparatively few occurring further than 5 in. from the edge of the stools. This implies that some factor, physical or chemical, encourages the females to oviposit close to the base of the cane stalks. Most of the eggs were found in the top 2 in. of the soil. Fewer were found in the next inch, and below this the numbers were negligible.

Kershaw (1913b) described the ovaries of *A. varia saccharina* and, because both have about 20 ovarioles with, in newly emerged females, each ovariole containing one mature and two immature eggs, presumed the maximum fecundity to be about 120 eggs laid in 3 successive batches. However, Fewkes (1963a, 1964a) showed that a female may lay as many as 294 eggs over a period of 3 to 4 weeks. Therefore, on average, each ovariole must be capable of developing 7 or 8 follicles. Fewkes (1964b) also showed that, in laboratory cultures, the average rate of oviposition varies seasonally, being highest (16–21 eggs/day) at the height of the wet season (August), and lowest (4–11 eggs/day) during the early part of the dry season (January, February). The lower rates of oviposition are correlated with the greater longevity (3–4 weeks) of dry season females (wet season females about 2 weeks). The only estimates of fecundity for other species are: 96 eggs for *A. flavilatera flavilatera* (James, 1946), 150 eggs for *A. varia sontica* (Guagliumi, 1962b) and up to 170 eggs for *Prosapia bicincta bicincta* (Byers, 1965).

4. The Egg Stage

Brief descriptions of the eggs of *Aeneolamia varia saccharina*, *A. varia sontica* and *A. flavilatera flavilatera*, were given by Kershaw (1913*b,c*), Guagliumi (1962*b*) and James (1946), respectively. Beck (1963) and Byers (1965) briefly described the eggs of *Prosapia bicincta bicincta*. From these descriptions and those of the eggs of other Cercopoidea (Ewan, 1961; Fewkes and Buxo, 1965; Weaver and King, 1954), it seems that egg shape, development and hatching mechanism vary little within the superfamily. The eggs are spindle shaped, and about three times as long as wide. The posterior end is blunt, and the anterior end tapers to a rounded point. A few days after oviposition, a dark longitudinal streak develops mid-dorsally beneath the chorion, extending from the anterior end of the egg along half its length. This streak has been called a hatching lid (Kershaw, 1913*b*; Williams, 1921) or an egg burster (Beck, 1963; Byers, 1965; Weaver and King, 1954). Later, the chorion splits longitudinally over the dark streak. Hatching generally occurs a few days afterwards.

Fewkes (1966) studied the eggs of *A. varia saccharina* in more detail. When laid, the eggs are pale yellow and typically spindle-shaped (0.75–0.90 by 0.25 mm). Within the chorion or egg shell is a relatively delicate inner membrane. A hatching line is evident in the chorion mid-dorsally, extending from the anterior tip along about half the length of the egg. At a later stage, a narrow, dark, elliptical area (the 'black lid') develops in the inner membrane beneath the hatching line and at the same time the inner membrane is strengthened, probably by the secretion of a



Fig. 1. The froghopper *Aeneolamia varia saccharina* (Dist.). Four empty egg shells, *above*, four eggs in an advanced stage of development, *below*. The chorions of the latter have split, exposing the 'black lid'. (Photo: B. H. Most)

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serosal cuticle. Before eclosion, the chorion splits along the hatching line, exposing the black lid, and the egg swells slightly (Fig. 1). During eclosion, the black lid breaks away from the inner membrane, fracturing along a line where it meets the unpigmented part of this membrane. The hatchling emerges head first from the egg, ventral side uppermost. An embryonic cuticle is shed at this time and is left with the egg shell and inner membrane, or near them. The black lid is not borne on the embryonic cuticle or on that of the first instar nymph. It is therefore not a typical egg burster (van Emden, 1946). It may, however, be responsible for the splitting of the chorion after which it serves as an operculum or egg cap.

During the development of *A. varia saccharina*, the germ band forms mid-dorsally, towards the posterior pole of the egg. The developing embryo turns into the yolk, tail end first, and stretches out within the egg in a reversed, inverted position. Later it reverts to its original orientation, with the head anterior and its ventral surface facing the dorsal ('lid') side of the egg. These movements of the embryo are indicated externally by the changing position of an orange-red pigment spot associated with its posterior end. At 23–27°C (mean, approximately 25°C) and under moist conditions, the pigment spot appears on the fourth day in a central position. In non-diapause eggs, movement of the spot to the anterior pole of the egg (5–10 days) generally precedes the first appearance of the black lid (7–8 days). Splitting of the chorion (9–10 days) coincides with movement of the pigment spot to the posterior (indicative of the turning of the embryo, or blastokinesis). The spot travels back until it is about 0.1 to 0.2 mm from the posterior pole. It then divides to form a pair of lateral spots in the embryonic abdomen. At about this time two eye spots appear at the anterior pole of the egg.

In eggs which enter diapause, the movement of the pigment spot to the anterior stops when it is about half way to the anterior pole, when development of the embryo apparently stops also. The black lid appears at the same time as in non-diapause eggs, so that the intermediate position of the pigment spot with the presence of the black lid beneath an intact chorion clearly indicates a state of diapause. Resumed movement of the pigment spot to the anterior marks the end of diapause. Arrival at the anterior pole is closely followed by backward movement of the spot (blastokinesis) and the simultaneous splitting of the chorion.

Most sugar cane froghoppers live in an environment that is only seasonally favourable for nymphal development. There is generally a fairly well defined dry season in sugar cane growing areas during which the crop is reaped. Populations of some species, notably *Aeneolamia varia* subsp. in Trinidad and Venezuela and *A. postica* subsp. in Mexico, survive this period as diapausing eggs in the cane field soil. The females of *A. flavilatera flavilatera* in Guyana lay a small proportion of diapause eggs, but their production does not apparently coincide with unfavourably dry conditions (James, 1946). The life cycles of *Prosapia bicincta bicincta* and *P. bicincta basalis* in the southeastern United States and Jamaica, respectively, also include a diapausing egg stage (Beck, 1963; Urich and Pickles, 1931).

The most detailed studies of egg diapause in sugar cane froghoppers have concerned *Aeneolamia varia saccharina* in Trinidad. Kershaw (1913b) found that although this species breeds throughout the dry season (January to May) amongst grasses in damp localities, some eggs remained dormant. Williams (1921) reported that many eggs laid in cane fields during October and November failed to hatch in the 2 or 3 months of wet weather that followed. Urich and Pickles (1930, 1931), studying the incubation of froghopper eggs laid at various times throughout the year and maintained in moist conditions, found that eggs of first-brood adults, laid during June and July, all hatched within 50 days. In contrast, complete hatching of eggs laid by adults of the subsequent broods took over 200 days. Only 50% of the eggs laid by second-brood adults (August, September) could have hatched in time to produce the third brood. Some of the remainder, and some of the eggs laid by third brood adults (October, November) would have hatched to give rise to a fourth brood. However, many of these eggs would have remained dormant in the soil over the dry season, not hatching until after the start of the rainy season in May and June of the following year.

The factors inducing diapause in froghopper eggs are unknown. In *Aeneolamia varia saccharina* occurrence of diapause and non-diapause eggs is not distinctly phased. The incubation period is variable, from 2 to over 40 weeks, throughout the year (Fewkes, 1963a, 1964b). The eggs of individual females, even eggs in the same batch, may differ widely in this respect. However, the average incubation period follows a fairly definite pattern, increasing from about 3 weeks in July to 7–10 weeks in November, and diminishing to about 5 weeks in March. There is some evidence that diapause is related to changes in day length, although these are relatively slight in the tropics, long days tending to prevent diapause (Fewkes, 1963a, 1964c).

The distinction between non-diapause and diapause eggs, in eggs laid at the same time, is quite clear in *Prosapia bicincta bicincta* because hatching takes place in two clearly separated periods. Temperature and moisture conditions immediately after oviposition appear to affect the proportion of eggs which enter diapause, low temperatures and dry conditions tending to increase the incidence of diapause (Byers, 1965).

Termination of diapause occurs without any apparent external stimulus in laboratory cultures of *Aeneolamia flavilatera flavilatera*, *A. varia saccharina* and *Prosapia bicincta bicincta* (James, 1946; Urich and Pickles, 1930, 1931; Byers, 1965). However, Fewkes (1963b) found that exposure of diapausing eggs of *A. varia saccharina* to dry conditions for 10 and 20 days accelerated the ending of diapause when moisture was again provided. It seems possible that, in the field, the synchronous hatching of eggs laid at various intervals prior to the onset of the rainy season may be favoured by dry spells.

Froghopper eggs may be exposed in the field to desiccation, flooding and high temperatures, and several authors have studied the effects of these on the

eggs of *Aeneolamia varia saccharina*. A moist atmosphere is required for full development and hatching of the eggs. Over a period of 3 months, no eggs hatched when held at 25% relative humidity, very few at 50% and 'a fair number' at 90%: in a saturated atmosphere, all eggs hatched (Hardy and Urich, 1927). Pickles (1932a) found that severe mortality occurred in eggs kept for 48 hours in relative humidities of less than 57%. Fewkes (1961, 1963b), however, recorded no significant mortality in diapause and non-diapause eggs exposed to dry conditions (30 to 40% r.h.) for periods of up to 20 days. The discrepancies between these results may possibly be explained by differences in the age of the eggs when first exposed to low humidities. In newly laid eggs the inner membrane is quite delicate but it is later strengthened, probably by the secretion of a serosal cuticle. The eggs of *Prosapia bicincta bicincta* will not hatch unless humidity is 100%. However, they can survive for at least 10 days in dry air (Byers, 1965). According to James (1946) the eggs of *Aeneolamia flavilatera flavilatera* are quite susceptible to dry conditions, severe and complete mortalities occurring at 14 and 28 days exposure (eggs kept in air-dried soil), respectively. Embryonic development stopped when the eggs were kept dry for 2 days and was resumed on remoistening. Fewkes (1963b) also found that the development of non-diapause eggs of *A. varia saccharina* was delayed by approximately the period of exposure to dry conditions.

Immersion of *A. varia saccharina* eggs in water for 14 and 18 days does not significantly affect their viability. Their development is delayed, but by only 2 or 3 days (Fewkes, 1961). James (1946) found that many of the eggs of *A. flavilatera flavilatera* could survive immersion in water for 90 days.

Exposure to a temperature of 60°C for 5 minutes is lethal to the eggs of *A. varia saccharina* (Urich and Hardy, 1928). Exposure to 50°C for 20 and 30 minutes killed most of the eggs, but some survived (Hardy and Urich, 1929a). At 45°C, most eggs survived for 2 to 3 hours. In Trinidad, during the dry season, this temperature is commonly attained at exposed soil surfaces in cane fields (Hardy and Urich, 1929b).

5. The Nymphal Stage

The nymphs of sugar cane (and other) froghoppers (Fig. 2) are characterised by their production of a frothy spittle or 'cuckoospit', in which they become enveloped. The functions of froghopper spittle are not fully understood, but it undoubtedly protects the pale, soft-bodied nymphs from desiccation. The spittle is formed from a viscous fluid which issues from the anus and is blown into bubbles by air from a ventral abdominal air chamber. The bubbles are distributed over the dorsal and lateral surfaces of the nymph by the mobile tip of its abdomen. The air chamber is formed by extensions of the tergites and pleurites of the abdominal

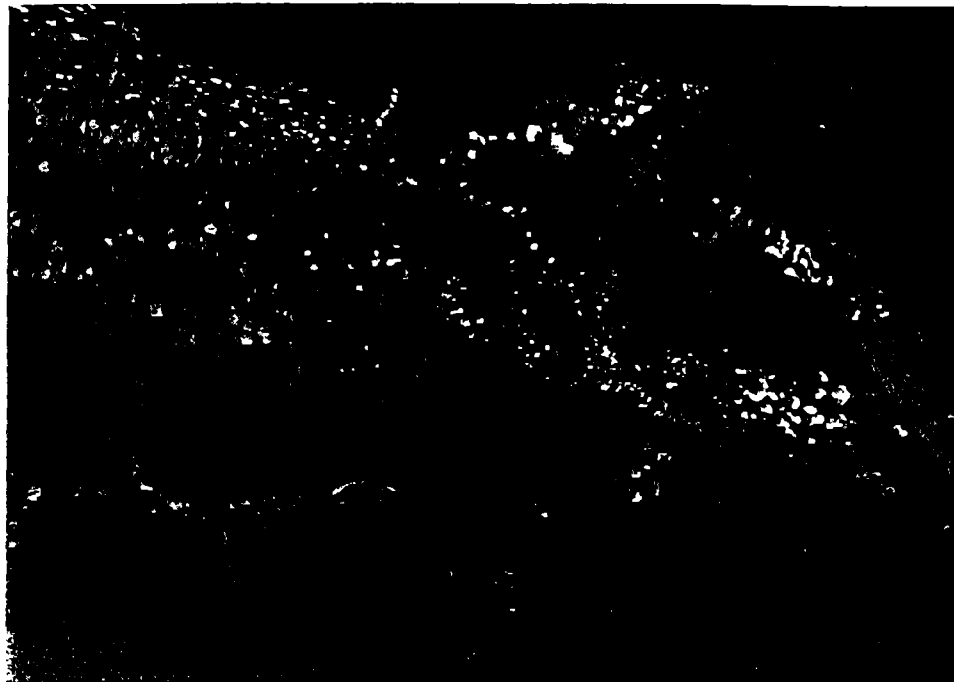


Fig. 2. The frog hopper *Aeneolamia varia saccharina* (Dist.). Fifth instar nymphs on sugar cane roots. Approx $\times 5$. (Photo: B. H. Most)

segments, which curve beneath the abdomen to meet in a mid-ventral line. The spiracles open into this cavity. The chamber is closed to the exterior, except for a posterior V-shaped valve through which air may be drawn in or expelled (Imms, 1957).

The anal fluid is mainly composed of the nymph's excretory products. In addition, a secretion from the anterior portions of the Malpighian tubules is present. This secretion, said to be a mucinoid (Kershaw, 1913*b*) or a mucocomplex (Marshall, 1964), is thought to impart stability to the froth. Ziegler and Ziegler (1958) estimated that over 90% of the organic matter in frog hopper spittle is protein.

The high protein content of the spittle led Ziegler and Ziegler (1958) to surmise that frog hopper nymphs feed in parenchyma or xylem tissues or that, alternatively, nitrogen-fixing symbiotic organisms, known to occur in some frog hoppers (Buchner, 1953) are involved. According to Esau (1961), frog hoppers of the genus *Aphrophora* are xylem feeders. Nymphs of *Philaenus spumarius* (L.) feed in the xylem of tomato plants (Wiegert, 1964). The feeding punctures of *Aeneolamia varia saccharina* nymphs terminate mostly in proto- or meta-xylem elements of sugar cane roots (Fig. 4a, b). During feeding, a salivary secretion is injected into the plant tissue and a salivary sheath is formed around the maxillary and mandibular



Fig. 3. The froghopper *Aeneolamia varia saccharina* (Dist.). Adult on a cane leaf. Approx. $\times 7$. (Photo: B. H. Most)

stylets. This stylet sheath is easily recognized in stained sections of roots, and clearly indicates where feeding has occurred (Hagley, 1966).

Xylem sap is a dilute watery solution, commonly containing inorganic salts of nitrogen, phosphorus, potassium and calcium, as well as various amino acids and sugars (Bollard, 1960). In order to obtain an adequate diet, large quantities of this sap must be ingested and a large volume of water eliminated. The alimentary canal of froghoppers is provided with a special filter chamber where the walls of the fore and hind guts are brought into close contact (Kershaw, 1914). This is presumed to allow the direct passage of excess water from the fore gut into the rectum, whilst the important nutrients pass, in a more concentrated form, through the main digestive and absorptive region of the mid gut.

Some sugar cane froghoppers feed as nymphs on the roots (e.g. *Aeneolamia* spp.), and others on the leaves (e.g. *Delassor tristis guppyi* and *Mahanarva indicata*) of their host plant. Nymphs of *Aeneolamia varia saccharina*, which normally feed on roots, will also feed on the leaves of sugar cane (Fewkes, 1964b), but after a few days, they practically cease to produce spittle and soon die. Presumably the xylem sap of the leaves provides an inadequate or unsuitable diet for the nymphs.

The effects of froghopper nymphs feeding on the roots of sugar cane are sometimes regarded as of minor importance (Guagliumi, 1962b; Pickles, 1937), probably because the damage caused by the adults feeding on the leaves is more

spectacular. Kershaw (1913b) found that nymphs of *Aeneolamia varia saccharina* feeding on young sugar cane plants cause a yellowing of the leaves. In heavy attacks the leaves turn yellow and then brown, eventually drying up, and the plant may be stunted. Caceres and Ruano (1961) stated that the feeding of nymphs of *Aeneolamia postica* subsp. causes a definite retardation in the growth of sugar cane. More recently Hagley (1966) observed that xylem elements punctured by frog-hopper nymphs often become occluded.

It is probable that most sugar cane froghoppers have five nymphal instars. This is only known to be so for two species: *Aeneolamia varia saccharina* (Fewkes, 1960) and *Prosapia bicincta bicincta* (Pass and Reed, 1965). However, five nymphal instars are recorded for a variety of Cercopoids (Bennett and Hughes, 1963; Ewan, 1961; Fewkes and Buxo, 1965; Kelson, 1964; Weaver and King, 1954). Metamorphosis is gradual. Later instars are distinguished from earlier stages by their increased size (particularly head width) and the development of the wing pads. When ready to emerge as adults, the nymphs of *A. varia saccharina* form a special 'froth chamber' in which the final moult takes place (Williams, 1921). The newly emerged adult remains within this chamber until its exoskeleton has hardened and darkened. Shortly after emergence, the adult voids a small quantity of a semi-solid white material that contains a high percentage (44%) of calcium phosphate (Kershaw, 1913b). This may be a form of storage excretion (Waterhouse and Day, 1953), or the disposal of material essential to the nymph for spittle production and no longer required by the adult.

6. The Adult Stage

Adult sugar cane froghoppers feed mainly on the leaves of the host plant. During the day the adults of *Aeneolamia varia saccharina* (Fig. 3) generally hide in the uppermost leaf axils ('funnels') of the cane plants (Williams, 1921). In sharp contrast to this behaviour, the adults of *A. flavilatera flavilatera* leave the sugar cane plants during the day to find shelter amongst grasses in the more open parts of a field and along the drains (Pickles, 1945). The adults of *A. varia saccharina* are most active at night, when they leave the cane funnels and begin to fly about. The greatest flight activity, judging by light trap catches, is in the first hour of darkness but light traps catch male froghoppers almost exclusively, so that their catches may not reflect a true pattern of adult activity (Williams, 1921).

Mating of *Aeneolamia varia saccharina* takes place during the day in the leaf axils of sugar cane (Smit, 1962), and also at night (Williams, 1921). In cages, mating may take place the day after emergence (Fewkes and Buxo, 1965). James (1946) reported that mating of *A. flavilatera flavilatera* may occur immediately after the adults have emerged from their froth chamber. There is some evidence that virgin females of *A. varia saccharina* secrete a sex attractant mainly during

the hours of darkness (Fewkes and Buxo, 1965). However, adults kept in insectary cages will mate more than once, and often do so during the day (Smit, 1962). Fertile eggs of *A. flavilatera flavilatera* and *A. varia saccharina* may be laid as early as 2 to 3 days after emergence (James, 1946; Author's unpubl. data).

A. varia saccharina adults feed at night (Williams, 1921) but also throughout the day (Author's unpubl. data). During feeding, adult froghoppers excrete copious amounts of a clear, watery fluid which is forcibly expelled in droplets from the anus (McLeod, 1908). These droplets probably consist largely of excess fluid that bypasses the mid gut, proceeding directly from the fore gut into the rectum via the filter chamber. There is no evidence of a mucocomplex secretion from the anterior portion of the Malpighian tubules as in the nymphs.

Unlike the nymphs, the adults of *A. varia saccharina* do not feed in the xylem of sugar cane. Withycombe (1926) found that the main effects of their sucking are on the border parenchyma cells of the vascular bundle. Hagley (1966) also found that most adult feeding-punctures terminate in the bundle sheath of cane leaves. It is here that the chloroplasts are concentrated, and the feeding of adult froghoppers may therefore be expected to have a direct effect upon photosynthesis. As

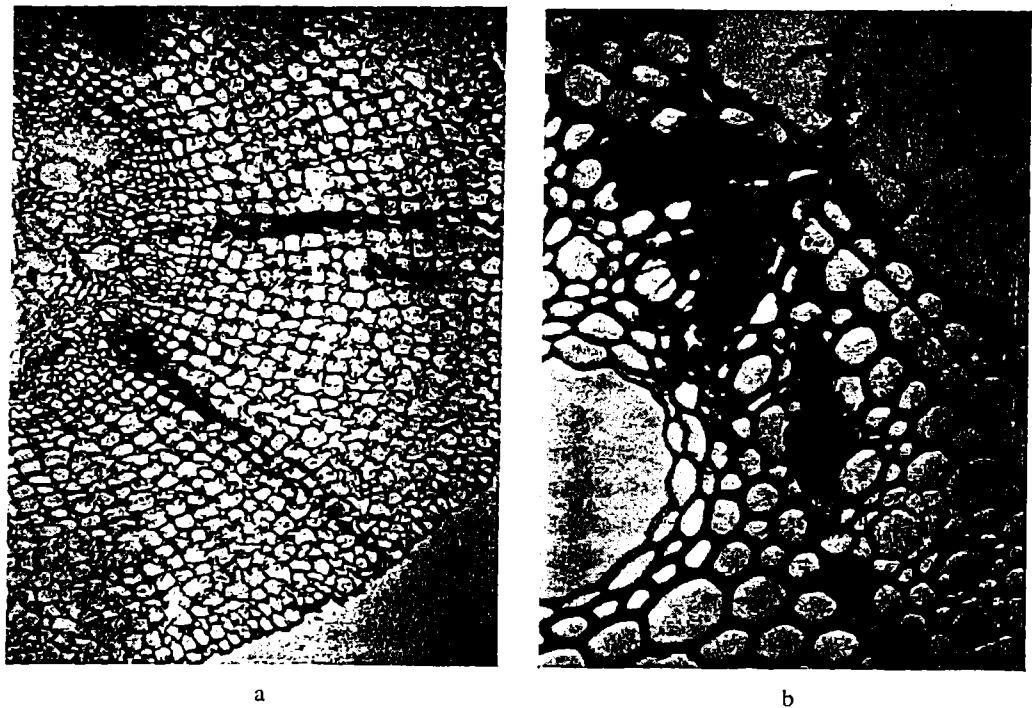
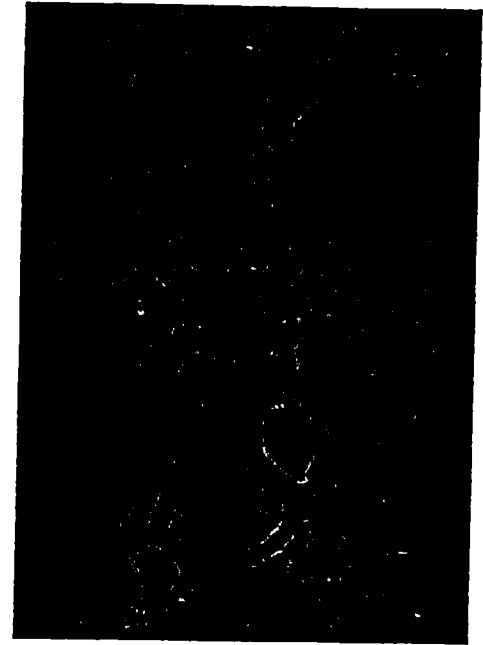


Fig. 4. Feeding sites of *Aeneolamia varia saccharina* (Dist.).

- (a) Transverse section of sugar cane root showing stylet sheaths of nymphs reaching to vascular tissues.
- (b) Ditto, showing multiple feeding probes of a fifth-instar nymph: the probes all end in xylem vessels: the disintegrated tissue at upper right is cortex.



c



d

(c) Tangential section of sugar cane leaf showing stylt sheath of adult ending in the border parenchyma: the stylets were inserted through a stoma.

(d) Transverse section of sugar cane leaf showing stylt sheath of adult ending in the border parenchyma: note the occluded phloem elements. (Photos: E. A. C. Hagley).

with the nymphs, a salivary secretion is injected into the feeding puncture, and a stylt sheath is formed (Fig. 4c,d).

It has long been recognized that the feeding of adult froghoppers is the main cause of froghopper 'blight' (Williams, 1921; Withycombe, 1926). Around each feeding puncture of *A. varia saccharina* the leaf tissue yellows, and a necrosis soon begins to develop. Over a period of 1 to 3 weeks the necrosis spreads longitudinally to form a brown streak of 'blighted' tissue (Fig. 5). The size and speed of development of a blight mark probably depends upon the duration and extent of the insect's feeding, as well as on the physiological state of the cane plant. When many punctures are present the blight streaks coalesce, and the whole leaf may be destroyed. The loss of photosynthetic tissue causes a severe retardation in the growth of the plant. Thin, stunted internodes are characteristic of blight-damaged sugar cane. In addition, the juice quality may be adversely affected.

The more or less gradual extension of blight streaks from feeding punctures suggests that the froghopper adult may inject a toxin or a disease organism into the cane leaf. Withycombe (1926) could find no evidence that any disease organism was transmitted during the feeding of *A. varia saccharina*. He stated that amylic

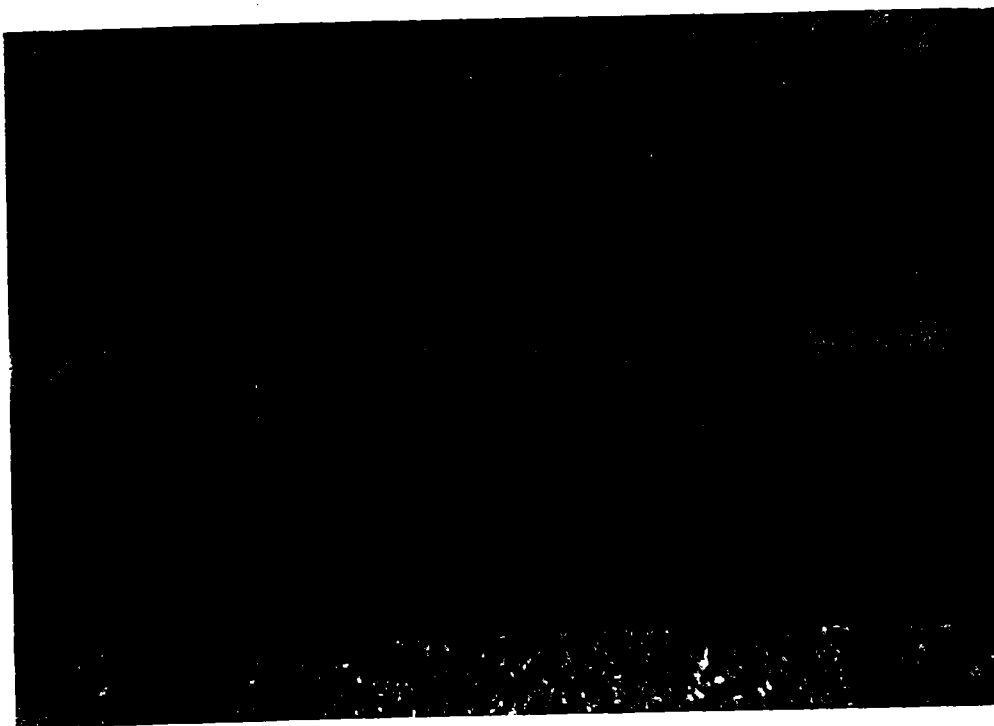


Fig. 5. Streaks of frog hopper blight caused by the feeding of *Aeneolamia varia saccharina* (Dist.) (Photo: B. H. Most).

and oxidizing enzymes secreted into the plant tissues during feeding were important factors in blight development. Pickles (1937) suggested that the saliva contains enzymes which may continue to break down leaf tissue after the frog hopper has finished feeding. Nuorteva (1956a) found that proteases were absent from the saliva of two Cercopoids, *Aphrophora alni* (Fall.) and *Philaenus spumarius* (L.), but Hagley (1967) showed that the saliva of *A. varia saccharina* adults contains an amylase, invertase, lipase, phenolase and proteinase. Artificial inoculation of a lipase into cane leaves produced fairly typical blight streaks, as long but not as wide as those resulting from the insect's feeding. Nymphs of *A. varia saccharina* placed to feed on sugar cane leaves did not cause typical blighting, although the nymphal saliva contains the same enzyme groups as found in the adult. This may be related to the site of feeding: most nymphal feeding punctures (80%) ended in the leaf parenchyma or the xylem, whilst the bundle sheath was only probed occasionally (17%). The salivary glands of *A. varia saccharina* are much larger in the adult than in the nymph. The main difference is in the length of the crown of tubular glands, which are short in 4th and 5th instar nymphs, but very long in the adult, extending far back into the abdomen (Kershaw, 1914). It seems possible that adults secrete larger amounts of saliva into the plant than do nymphs.

Williams (1921) and Urich (1928) considered that the saliva of *A. varia*

saccharina may contain a toxin. Fewkes and Cutler (1963) found that fresh extracts of salivary glands of adults of this species promoted the growth of *Avena* coleoptile sections in the dark. This was confirmed by Fewkes and Most (1964), who also found that the extract was rich in ninhydrin-positive substances, probably amino acids. At certain concentrations, such substances might well be toxic to plant tissues. Hagley (1967) identified 17 amino acids in the salivary glands of *A. varia saccharina* adults. Artificial inoculation of sugar cane leaves with an amino acid mixture, containing 2 mg/ml each of alanine, aspartic acid, glycine, phenylalanine, proline, tryptophan and valine, caused red streaking typical of early blight development. The possibility that the saliva contains growth hormones is presently under investigation. Nuorteva (1956b) suggested that, by injecting toxic substances, a sucking insect might cause an upset in the host plant which would increase its nutritional value to the insect. When feeding in the bundle sheath, it may well be advantageous for adult froghoppers to upset the movement of nutrients into the vascular bundles from this actively photosynthesizing tissue.

Froghopper adults are capable of leaping as well as flying, the back legs being specially adapted for this. Hopping is an escape reaction. Flight leads to dispersal. In Trinidad, re-infestation of plant cane fields by *Aeneolamia varia saccharina* is almost entirely dependent upon adult migration, as the resident egg population is largely destroyed by ploughing (Pickles, 1933b). Most flights take place at night, when the adults are often attracted to light (Williams, 1921). Smith (1926) stated that migration assumes the form of a drift from field to field and saw froghoppers perform flights of 70–80 ft. In British Honduras, adults of *Aeneolamia postica jugata* are said to migrate from bush areas into cane fields over a distance of about 40 ft (Fewkes and Buxo, 1965). Pickles (1931d) found that as many adults of *A. varia saccharina* entered as left blighted areas. On the other hand, about twice as many entered than left an unblighted field. The invading froghoppers apparently approached the field from all sides, and the direction of flight could not be correlated with wind direction. However, Fewkes and Buxo (1965) found that in a large plot experiment, where strips of sugar cane treated for nymph control were separated by untreated strips, more adult migration took place from the windward than from the leeward sides of the infested plots into the insecticide-treated plots.

7. Life Cycle

All sugar cane froghoppers that have been studied have two or more generations a year. In most species, the annual cycle is interrupted by a diapausing egg stage. Some species are capable of breeding all the year round, but the dry season and coincident harvesting period usually interrupt this continuous cycle in sugar cane. Generation time is very variable, depending upon the duration of egg diapause. When development is direct, most species complete

TABLE 2

THE MOST IMPORTANT NATURAL ENEMIES OF SUGAR CANE FROGHOPPERS

Species	Froghopper and stage attacked	Reference
HYMENOPTERA		
Eulophidae		
<i>Centrodora perkinsi</i> Waterst.	<i>Aeneolamia flavilatera</i> <i>flavilatera</i> (egg)	Guagliumi (1962b)
<i>C. tomaspidis</i> (How.)	<i>Aeneolamia varia</i> <i>saccharina</i> (egg)	Urich (1915)
Mymaridae		
<i>Acmapolynema hervali</i> Gomes	<i>Sphenorhina liturata</i> (egg)	Gomes (1948)
<i>Anagrus flaveolus</i> Waterh.	<i>Aeneolamia varia</i> <i>saccharina</i> (egg)	Pickles (1938)
<i>A. urichi</i> Pickles	<i>Aeneolamia varia</i> <i>saccharina</i> (egg)	Pickles (1932b)
<i>Anagrus</i> sp.	<i>Aeneolamia lepidior</i> (egg)	Williams (1921)
Trichogrammatidae		
<i>Abella tomaspidis</i> Pickles	<i>Aeneolamia varia</i> <i>saccharina</i> (egg)	Pickles (1932b)
<i>Lathromeris</i> sp.	<i>Aeneolamia varia</i> <i>saccharina</i> (egg)	Hardy and Rodriguez (1930)
<i>Oligosita giraulti</i> Crwf.	<i>Aeneolamia flavilatera</i> <i>flavilatera</i> (egg)	Williams (1921)
	<i>Aeneolamia varia</i> <i>carmodyi</i> (egg)	Williams (1921)
	<i>Aeneolamia varia</i> <i>saccharina</i> (egg)	Urich (1913a)
<i>Oligosita</i> sp.	<i>Aeneolamia varia</i> (egg)	Guagliumi (1962b)

their life cycle in about 2 months. When diapause is prolonged, the full cycle may take as long as 9 months or more. Where such protracted diapause occurs, only a small proportion of the eggs is involved, so that shorter cycles are more typical. In the southeastern United States, *Prosapia bicincta bicincta* has two generations a year, the cycle being interrupted by cold weather (Beck, 1963; Byers, 1965). The number of generations of *Aeneolamia postica* subspp. in Mexico varies from two in the north-west to four in the south. The number is apparently limited by the duration of the dry season, which ends in May in southern Mexico, but extends into July in the north (Caceres and Ruano, 1961; Iturbe and Ruano, 1963). In British Honduras *Aeneolamia postica jugata* appears to have only two generations a year in sugar

TABLE 2 Continued.

Species	Froghopper and stage attacked	Reference
DIPTERA		
Syrphidae		
<i>Salpingogaster nigra</i> Schiner	<i>Aeneolamia flavilatera</i> <i>flavilatera</i> (nymph)	Williams (1918)
	<i>Aeneolamia lepidior</i> (nymph)	Williams (1921)
	<i>Aeneolamia postica</i> subsp. (nymph)	Williams (1921)
	<i>Aeneolamia varia</i> subsp. (nymph)	Guagliumi (1962b)
	<i>Aeneolamia varia</i> <i>saccharina</i> (nymph)	Urich (1913b)
NEMATODA		
Mermithidae		
<i>Hexameris</i> sp.	<i>A. varia saccharina</i> (nymph, adult)	Urich (1915)
	<i>A. varia</i> subsp. (nymph, adult)	Guagliumi (1962b)
FUNGI		
Entomophthoraceae		
<i>Metarrhizium anisopliae</i> (Metch.)	<i>Aeneolamia varia</i> <i>saccharina</i> (adult)	Urich (1915)
	<i>Aeneolamia varia</i> subsp. (adult)	Guagliumi (1962a)
<i>Empusa</i> sp.	<i>Aeneolamia varia</i> <i>saccharina</i> (adult)	Urich (1915)

cane, cold weather in October and November and a severe dry season from January to May limiting the number of cycles (Fewkes and Buxo, 1965). The various subspecies of *Aeneolamia varia* in Venezuela and Trinidad are capable of breeding throughout the year, wherever conditions are suitably moist. This is because the females commonly lay some non-diapause, together with diapause eggs (Fewkes, 1964c). In damp, grassy areas six generations may occur. However, in sugar cane, the number of generations is usually limited to four, as there are several months (February to April) when there is insufficient moisture for egg and nymphal development. In Guyana and Venezuela, *Aeneolamia flavilatera* subsp. breed throughout the year in suitably damp locations. Although some diapause eggs are

produced, the insects apparently depend mainly upon migration to re-infest habitats, such as sugar cane fields, that periodically become unsuitable for their development (James, 1946; Guagliumi, 1962b).

In Trinidad and Venezuela, the 'first' brood populations of *Aeneolamia varia* subsp., which develop shortly after the start of the rainy season, are usually small (Williams, 1921; Guagliumi, 1962b). There is often a large increase in numbers in the 'second' brood. In a population study of *Aeneolamia varia saccharina* in Trinidad, Fewkes (1961) recorded an increase of from 17 adults/cane stool (maximum) in the first brood, to over 200 in the second. The study was terminated before the peak of the second brood adult population, as serious blighting of the cane had occurred. Third-brood infestations of *A. varia saccharina* may also be high (Williams, 1921), but the fourth brood is normally small. This is probably due to the deposition by third-brood females of a high proportion of diapause eggs.

8. Natural Enemies

Natural enemies of sugar cane froghoppers are recorded only in the New World. Most of those recorded are non-specific predators that occasionally take froghoppers, and are not included in Table 2, which lists the more or less specific predators and parasites. The eggs are parasitized to a limited extent by various Chalcidoids. The most important enemy of the nymphs is the larva of a Syrphid, *Salpingogaster nigra* Schiner. However, this predator is itself parasitized by an Encyrtid, *Aphidencyrtus* sp. (James, 1946). An entomogenous fungus, *Metarrhizium anisopliae* (Metch.), is the main natural enemy of the adults. In addition, a parasitic nematode, *Hexamermis* sp. (Mermithidae), has been found in fifth-instar nymphs and adults of *A. varia saccharina*. Apart from the more or less specific natural enemies, various insects, spiders, frogs, toads, lizards and birds occasionally prey on nymphs and adults of sugar cane froghoppers (Williams, 1921; Guagliumi, 1962b). Pickles (1933a) pointed out that, in Trinidad, the climatic conditions in sugar cane plantations are much less favourable to the most important natural enemies of froghoppers than to the froghoppers themselves. This has resulted in the development of a serious pest problem. The same is probably also true for South and Central America and for Mexico.

9. Summary

Most of the species and subspecies of froghoppers known to feed on sugar cane belong to the family Cercopidae. Sugar cane froghoppers of economic importance do not occur outside the New World. Since sugar cane was introduced

into this area, several of the native froghoppers have become adapted to it as their main host plant. There is some evidence that they are attracted to sugar cane by its leaf odour. The most important genus is *Aeneolamia*, species of which are serious pests of sugar cane in Mexico, Venezuela and Trinidad.

The eggs are laid in soil or in plant tissue, their position usually being correlated with the nymphal feeding site. The eggs are spindle shaped, about 3 times as long as wide. Before hatching, a hatching lid, formed beneath the chorion during egg development, is exposed by splitting of the chorion. Movements of the embryo within the egg are indicated by changes in the position of a pigment spot associated with its posterior end. During unfavourable dry periods some species survive as diapausing eggs in the soil. The duration of diapause is very variable, and a female may lay non-diapause and diapause eggs even in the same batch. There is some evidence that the average duration of diapause is related to day length, long days tending to prevent diapause. The eggs of some species are very resistant to desiccation, flooding and high temperatures.

The nymphs are characterized by the production of a froth or 'spittle' which probably serves to protect them against desiccation. The spittle is formed from bubbles of a liquid containing the excretory products and a special secretion from the Malpighian tubules which is said to be a mucocomplex imparting stability to the froth. The nymphs of some species feed in the xylem of sugar cane roots. This may cause a yellowing of the leaves, and sometimes a general stunting of growth.

Sugar cane froghopper adults feed on the leaves of their host plant. They generally hide in the uppermost cane leaf axils in daytime and are more active at night. Mating occurs at all times of the day and night, but there is some evidence that virgin females release a sex attractant at night. Copulation may occur on the same day as adult emergence, and fertile eggs may be produced within 3 days of first mating. The adults feed on the border parenchyma of sugar cane leaves, where most of the chloroplasts are found, causing 'blight' of the leaves. This blight is a necrosis which develops from each feeding puncture and spreads longitudinally. There is no evidence that a disease organism is introduced during feeding, but it is thought that the salivary secretion of adult froghoppers contains a substance or substances toxic to the host plant. Amino acids and enzymes, particularly a lipase, may be implicated.

Dispersal takes place in the adult stage. Migration seems to be short range and non-directional. Adults tend to leave heavily infested fields to settle in fields with low froghopper populations.

The duration of the life cycle varies considerably, depending upon the occurrence and duration of egg diapause. Without diapause it is generally about 2 months. Breeding may proceed throughout the year in warm, moist habitats, but is usually interrupted in sugar cane by a dry season. The first brood, which appears soon after the first rains, is usually small but may often give rise to a very large

second brood. Further broods occur where conditions remain favourable, but are usually smaller, due to the deposition of an increasing proportion of diapause eggs.

A large number of natural enemies is recorded for the New World sugar cane froghoppers. Most of these are non-specific predators which do not seem to have much effect in reducing froghopper populations. The more important natural enemies include several Hymenopterous egg parasites, a Syrphid predator of the nymphs, and an entomogenous fungus that attacks the adults. These natural enemies seem to have become less well adapted to the ecological conditions in sugar cane plantations than have the economically important sugar cane froghoppers.

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The Control of Froghoppers in Sugar Cane Plantations

D. W. FEWKES

*Tate and Lyle Central Agricultural Research Station, Carapichaima, Trinidad**

1. Introduction

Sugar cane was introduced into the New World in the 16th and 17th centuries. Since then, several indigenous species of froghoppers, which fed on various native grasses and sedges, have become adapted to sugar cane as their main host plant. This adaptation was gradual. The earliest records of 'froghopper blight' of sugar cane are from Trinidad in 1863 (Hart, 1890) and from British Honduras in 1883 (Williams, 1921). Since 1900, froghoppers have become major pests of sugar cane in Trinidad, Venezuela, Mexico, Brazil, British Honduras and, to a lesser extent, in Guyana.

Although it is common experience that froghopper infestations damage sugar cane and cause reduced yields, and sometimes devastate crops, there have been very few estimates of yield losses. Data from a large plot ($\frac{1}{2}$ acre) experiment in Trinidad, indicated that moderate froghopper blight damage reduced sugar yields by some 40% compared to yields from unblighted plots (Merry *et al.*, 1963). Further experiments have indicated that losses in excess of 1 ton sugar/acre are common in blighted cane (Fewkes and Buxo, 1966c). There is therefore a very great need for effective sugar cane froghopper control.

Insect control is essentially a problem of population dynamics but there have been very few attempts to study sugar cane froghopper populations and the factors that regulate them. Some measure of control has been achieved by the use of insecticides, and much of the work on sugar cane froghoppers has concerned this aspect. In addition, some attempts have been made to find biological and cultural methods of control. More basic studies on egg diapause, sex and oviposition attractants, and nutritional aspects of the plant-insect relationship are in progress (Vlitos, 1959; Fewkes, 1960, 1961a, 1963, 1964; Fewkes and Buxo, 1965a; Fewkes *et al.*, 1966). Although aimed at developing new methods of control, these studies are not discussed here. For the most part therefore, this article is concerned with the methods used to protect sugar cane from froghopper damage.

*Now at Tate & Lyle Research Centre, Westerham Road, Keston, Kent, England.

2. Chemical Control

Insecticides and techniques

The annual development of sugar cane froghopper infestations follows a similar pattern in British Honduras, Mexico, Trinidad and Venezuela (Fewkes and Buxo, 1965a; Caceres and Ruano, 1961; Williams, 1921; Guagliumi, 1962). The insects pass the dry ('winter') season in a diapausing egg stage. The first ('spring') brood, which hatches soon after the start of the rainy season, is usually small and rarely causes serious damage to sugar cane. However, if this brood is allowed to develop unchecked, it may give rise to extremely heavy second brood infestations. In Trinidad, Venezuela and southern Mexico, there is also a third brood that, although generally smaller, may equal or surpass the second brood in size. A small fourth brood occurs in some areas. Most eggs laid by adults of the first brood develop without a diapause. Those laid by adults of succeeding broods include an increasing proportion of diapause eggs. Many of these are destined to remain dormant in the soil until the start of the rainy season in the following spring.

Effective control of the first brood should theoretically prevent further broods, unless re-infestation occurs by migration from untreated areas. However, it has generally been impracticable to treat all froghopper-infested fields during the first brood, as the period for effective control is limited to 3 or 4 weeks. Also, the first brood infestations are generally low and may escape attention. Therefore control of the second brood is more commonly practised.

All early work on chemical control of sugar cane froghoppers was done in Trinidad and the methods developed there have been adopted, with minor modifications, elsewhere. These methods are described below, country by country. Approved common names of the insecticides, as listed by Billings (1963, 1964), have been used where possible, except that benzene hexachloride has been abbreviated to BHC. Wherever rates of application are given they refer to active ingredient (not commercial formulation), unless otherwise stated.

Trinidad — Froghoppers, *Aeneolamia varia saccharina* (Distant), have been known to cause 'blight' of sugar cane in Trinidad since 1863. Several severe outbreaks occurred in the period 1900 to 1918 (Williams, 1921), and since then the insect has posed an annual threat to sugar production. At the time of the first outbreaks, chemical control of insects was in its infancy. The earliest attempts at chemical control of sugar cane froghoppers involved the use of cyanogas against the nymphs (Follett-Smith, 1926; Hardy, 1926a,b,c). Cyanogas A dust (a powder containing 50% calcium cyanide) was applied at 30 lb/acre with manually operated dusters around the bases of infested cane stools. This treatment proved effective in destroying nymphs exposed at the soil surface, but did not kill those concealed in cracks in the soil. Cyanogas was also effective as an ovicide (Rodriguez,

1928). It had, however, no residual effect and unless the treatment was applied at the peak of an infestation, just before the main adult emergence, many nymphs survived and a further treatment was required. In a widespread outbreak it was not possible to treat all affected fields at the correct time (Pickles, 1938). Despite these limitations, cyanogas was used widely to control frog hopper for about 15 years.

Tests with pyrethrum during 1936 and 1937 indicated that it could be used to destroy adult frog hoppers (Pickles, 1938). During 1939 and 1940 frog hopper control was achieved in some areas by the application at night of a pyrethrum powder diluted with sulphur. The dust was blown from tractor-mounted and powered dusting machines, and allowed to drift over the cane fields with the light evening breeze. A high mortality of adult frog hoppers resulted from this treatment (Pickles, 1942). However, several applications were required for adequate control of heavy infestations. Use of cyanogas against the nymphs, and 'drift dusting' with pyrethrum to control any adults which subsequently emerged, gave the best results.

In further experiments with drift dusting, Pickles (1946) found that DDT (4%), sabadilla (30%) and DDT-sabadilla (4+30%) mixture gave good control of adult frog hoppers. DDT proved slow acting but had some residual effect. Sabadilla, like pyrethrum, gave a quick knockdown but showed no residual activity.

Blackburn (1949) reported that drift dusting with Agrocide 3 (0.65% *gamma* BHC) or 6% DDT at 30 lb/acre, during 1947, gave excellent control of frog hopper adults up to 250–350 ft from the point of application in the windward 'trace' (field interval). Beyond this distance the treatments were much less effective, so that the western (leeward) halves of some fields became badly blighted. Use of fogging equipment (Todd Insecticidal Fog Applicator) to apply DDT in oil, proved much less effective, control being limited to 40–60 ft from the field edge. Better results were obtained with applications of *gamma* BHC and DDT dusts by helicopter. However, there was very little residual effect, and it was estimated that several applications at 3 to 6 day intervals would be necessary for the control of heavy frog hopper infestations.

Potter and Carrington (1947) found that application of Agrocide 2 (0.46% *gamma* BHC) as a root dust, gave excellent control of frog hopper nymphs for a period of 3 months. A further experiment in 1948 indicated that applications of *gamma* BHC diluted to 0.52% with pulverized limestone (100 mesh), at 1, 3 and 6 cwt/acre, completely controlled first brood nymphs and maintained control throughout the season (Potter and Carrington, 1949). Blackburn (1949) also found that root dusting with *gamma* BHC (0.65% in ground limestone at 1 cwt/acre) provided excellent initial and residual control of frog hopper nymphs. DDT (5% in ground limestone at 1 cwt/acre) gave inferior results. Little (1953) reported that dieldrin (at 1 lb/acre) was also effective as a root dust against frog hopper nymphs. Extension of these findings into routine estate practice resulted in effective economical control of frog hopper infestations over the next 5 years. In 1954, it was

noted that in some areas frog hopper nymphs were resistant to *gamma* BHC (Blackburn, 1954). This resistance extended to dieldrin, aldrin and chlordane, and, it was thought, to other organochlorine insecticides. Resistance to dieldrin was reported in 1956, but the dieldrin-resistant nymphs were apparently still susceptible to *gamma* BHC (Little, 1958).

Malathion (3% in ground limestone at 280 lb/acre) proved effective against the *gamma* BHC-resistant nymphs, but showed poor residual activity. Several applications were needed for satisfactory control. From 1955 to 1957, frog hopper resistance to *gamma* BHC became increasingly apparent. Several organophosphate insecticides were tested for frog hopper nymph control, but only one, carbophenothion (trithion) (2% in ground limestone at 280 lb/acre), exhibited prolonged residual activity as a root dust (Neate, 1958). This insecticide was slow acting and expensive compared with *gamma* BHC, but proved equally effective in residual control of nymph infestations on an estate scale.

During 1959 to 1960, isobenzan (telodrin), phorate (thimet) and carbaryl (sevin) were also found to be effective in frog hopper nymph control. The rotational use of carbamate, organophosphate and organochlorine insecticides was recommended as most likely to delay or prevent the selection of strains of frog hopper resistant to any one of them (Merry *et al.*, 1963). After a period of 4 to 5 years in which organophosphate (carbophenothion and phorate) and carbamate (carbaryl) insecticides were widely used for frog hopper control, it was found that the nymphs were again susceptible to DDT (Vlitos and Merry, 1962) and to *gamma* BHC (Lawrie *et al.*, 1964; Fewkes and Buxo, 1965a; Fewkes and Lawrie, 1967). Two other organochlorine insecticides, endosulfan (thiodan) and toxaphene, were also found to be effective in nymph control. This apparent instability of resistance to organochlorine insecticides in frog hoppers lends support to the theory that a rotational use of insecticides having different modes of action may avert the development of resistance to insecticides (Lewallen, 1960). The prolonged use of any one type of insecticide would best be avoided. Another approach, suggested by Vlitos and Merry (1962), is to use combinations of organochlorine with organophosphate or carbamate insecticides (e.g. DDT with malathion or carbaryl).

In Trinidad, cane trash (dead leaf tissue) is burnt both before and after harvest. However, by the time that most fields are treated for frog hopper nymph control (August and September), a considerable amount of trash is usually present. Removal of weeds and trash from the bases of cane stools, prior to the application of an insecticide, has generally been considered necessary for good nymph control (Follett-Smith, 1926; Hardy, 1926a,b,c; Blackburn, 1949; Potter and Carrington, 1949; Merry *et al.*, 1963). However, Little and Johnson (1963) and Merry *et al.* (1963) found that the systemic insecticide phorate gave equally good results in the presence or absence of cane trash. Further studies have indicated that some non-systemic insecticides (e.g. carbophenothion, and endosulfan) may be used successfully over trash, if they are applied directly into the stool bases (Lawrie

et al., 1964; Fewkes and Buxo, 1965a, 1966a). Others, such as *gamma* BHC, gave inferior nymph control when applied over trash.

More recently, control of froghopper infestations by applying liquid sprays of insecticides from the air has been investigated (Fewkes and Buxo, 1965b, 1966b). The insecticides, diluted with water, were applied by helicopter at 2–4 gal (U.S.)/acre as foliar sprays for control of adult froghopper populations. Applications of carbaryl (85% 'sprayable' formulation), at 2, 3 or 4 lb/4 gal (U.S.)/acre, gave excellent control of first brood adults. When the application was timed correctly, destroying the adults before many eggs had been laid, the second brood infestation was negligible. Similar results were obtained with and without the addition of the sticker UCAR 680 (Union Carbide) at 4 ml/lb carbaryl. When applications were made too late to prevent the adults from laying a large proportion of their eggs, heavy second brood infestations developed.

Applications of imidan (50% wettable powder formulation) from the air at 2 lb/2 gal (U.S.)/acre gave excellent control of second brood adults, and were also effective in controlling froghopper nymphs at the roots of sugar cane. A special sticker for imidan, R.F. No. 1618 (Stauffer Chemical Co.), was incorporated in the spray solution at $\frac{1}{2}$ pt/gal (U.S.). Imidan is not a systemic insecticide, and its effect on nymphs must be due to rain washing it to the ground. However, sufficient insecticide remained on the leaves 9 days after application to kill adult froghoppers. Similar but slightly inferior results were obtained with a systemic insecticide, dimethoate (3 lb/imp. gal liquid formulation), at 3 lb/3 gal (U.S.)/acre. Aerial applications of granules of another systemic insecticide, phorate, at 2.5 lb/acre (25 lb of a 10% granular material), were also tested for froghopper control. This treatment gave effective control of both nymphs and adults in the second brood.

On a cost-performance basis, the treatments with carbaryl and imidan were superior to those with dimethoate and phorate. If these treatments are applied, with correct timing, to sufficiently large blocks of sugar cane (rather than on an individual field basis), to reduce the chances of re-infestation by migrants, they may be expected to provide effective, economical control of sugar cane froghoppers. However, the total biological effects of such large scale aerial treatments cannot be forecast. If this method of froghopper control is adopted, careful studies should be made of its effect on beneficial and potential pest species.

During 1966 an attempt was made to control froghopper infestations from the air over a 3,700-acre block of sugar cane (Fewkes and Buxo, 1967). The insecticides (carbaryl, imidan and malathion LVC) were applied from a fixed wing aircraft (Piper Pawnee). The whole ratoon acreage (3,300 acres) was treated once in the first brood, mainly with carbaryl (2.5 lb/3 gal (U.S.)/acre). Some areas required further treatment in the second brood because the timing of the first brood sprayings did not allow for a prolonged emergence of the first brood adults (from early June to mid July), and most fields were resprayed in the third brood. On average, 3.3 sprayings per acre were applied to ratoon cane, but none

of the plant cane fields (400 acres) needed treatment. Excellent control of froghopper infestations was achieved at about half the cost of routine methods (i.e. nymph control with carbophenothion or toxaphene). For future years it is recommended that a more rigorous control of the first brood should be attempted, with two sprayings where necessary.

Venezuela — According to Pickles (1944) froghoppers have been known to attack sugar cane in Venezuela since about 1913. However, these pests (*Aeneolamia varia* (F.) subsp., especially *A. varia sontica* Fennah) did not become a major problem until 1945 to 1946 (Guagliumi, 1954a). Over the next 5 years, control was achieved by the application of dusts or sprays of *gamma* BHC and DDT against the adults. Treatments were applied from the ground with various hand-operated and motorised machines, and later from the air. This method of controlling froghoppers proved very effective but, because of the short residual effectiveness of the treatments, 2 to 4 applications were required for control of the second brood.

Fénjves (1950) suggested that the method developed in Trinidad of destroying froghopper nymphs, especially those of the first brood, with *gamma* BHC, should be tried in Venezuela. Guagliumi (1954b) stated that this method of control was the most effective, for one application often gave season-long control. The same author later recommended the use of a granular formulation of *gamma* BHC for nymph control (Guagliumi, 1958). For adult control, he found that a mixture of *gamma* BHC and methyl parathion dusts (1.5 + 1%), applied at 30 kg/ha, gave excellent results. Guagliumi (1962) has also recommended the use of a mixture of two insecticides, one fast acting and the other having a long residual effect (e.g. an organophosphate and an organochlorine), for the control of heavy second brood nymph infestations. So far, there have been no reports of resistance to *gamma* BHC in Venezuelan sugar cane froghopper populations.

Mexico — Williams (1921) stated that sugar cane and pastures in Mexico had been damaged by froghoppers (*Aeneolamia postica* (Wlk.) subsp.) for many years. However, the first serious damage to sugar cane occurred in 1943 (Caceres and Ruano, 1961). In the next 7 years, the pest spread throughout the sugar cane growing areas, and by 1951 almost every plantation was affected.

Until 1952, insecticides (*gamma* BHC and DDT) were used mostly to control adult froghoppers. This was considered unsatisfactory, as control was achieved after the nymphs had damaged the root system and after some injury to the leaves had been caused by adult feeding. After 1952 nymph control by root dusting with *gamma* BHC was generally adopted (Iturbe and Ruano, 1963). Satisfactory results were obtained with applications of 1% (at 100 kg/ha) or 3% (at 30–50 kg/ha) dusts (80 to 100 mesh) of *gamma* BHC. Aldrin (3%) dieldrin (2.5%), isobenzan (2%), carbaryl (7.5%) and phorate (5%) dusts, applied at 25 kg/ha, have also given good control of nymphs. However, *gamma* BHC is still preferred because of its low cost. Where adult control is necessary, aircraft are used to apply a finer (200 to 300 mesh) 3% dust of *gamma* BHC, at 30 kg/ha. So far there have been no signs of

resistance to *gamma* BHC amongst Mexican sugar cane froghoppers.

Brazil — The most important froghopper pest of sugar cane in Brazil is *Mahanarva indicata* Distant. Although known from Brazil since 1921, this species was not recognised as a serious pest of sugar cane until 1954 to 1956 (Albert, 1964). Control has been achieved by aerial applications of carbaryl (5%) and *gamma* BHC (3%) dusts. These treatments destroy both adults and nymphs, because the latter are found high up in the leaf axils of the plants. Small outbreaks are controlled by application of the same insecticides from the ground, using motorised dust applicators.

Other species of froghoppers known to attack sugar cane in Brazil are: *Tomaspis entreriana* Berg, *T. flavopicta* (Stål), *T. furcata* (Germ.), *Sphenoclypeana parana* (Dist.) (Tomaspidini), *Aeneolamia astralis* (Dist.), *Delassor rubicundus indentatus* (Walk.), *Deois knoblauchii* (Berg), *Sphenorhina liturata ruforivulata* (Stål) and *S. rubra sororia* (Germ.) (Cercopini) (Box, 1953). Control where necessary is effected by aerial applications of insecticides, mainly *gamma* BHC (Dantas *et al.*, 1952).

British Honduras — In British Honduras, infestations of froghopper (*Aeneolamia postica jugata* (Fowler)) nymphs are controlled by root dusting with 5% *gamma* BHC at 30 lb/acre (Fewkes and Buxo, 1965a). The most troublesome attacks are from adult froghoppers, which fly into the sugar cane fields from uncultivated ('bush') areas. Such infestations are generally controlled by drift dusting with malathion (25% dust base) at 0.5–1 lb/acre. More recently malathion dust (25%) has been applied from the air for control of adults, with satisfactory results (O.M. Seaton, *in litt.*).

Guyana — The Demerara sugar cane froghopper, *Aeneolamia flavilatera flavilatera* (Urich), was first found to attack sugar cane in 1909 (Urich, 1914a) but did not cause serious injury to sugar cane until 1943 (Pickles, 1945). Attempts to control the nymphs with applications of cyanogas gave rather unsatisfactory results. James (1946) recommended the use of 0.5% *gamma* BHC (at 20 lb/acre) as a drift dust for control of adult froghoppers. However, this method was found to give poor control and was discontinued by 1950 (Bates, 1958). Since then the pest has been controlled by hand dusting or spraying and by aerial application of insecticides. For nymph control *gamma* BHC diluted with pulverised limestone (100 mesh) is spread by hand. Aerial applications of *gamma* BHC or dieldrin, at as little as 6pt/acre, are used for adult control. In general, outbreaks of this froghopper are sporadic, and it is nowadays considered as a relatively minor pest (Bates, 1967).

Assessing results of treatments

The effectiveness of treatments applied on a field scale for froghopper control may be assessed by their ability to prevent blight. "Check areas" which have not

been treated with insecticides for frog hopper control are generally available in Trinidad, in the form of some peasant farmers' cane fields. These are often severely blighted and indicate clearly the value of effective frog hopper control.

The total biological effects of the insecticide treatments have nowhere been carefully studied. No undesirable side effects on other insects have been noted from root dusting. In Trinidad, intensive drift dusting with DDT is said to have caused an increase in the damage to sugar cane from moth borers, particularly *Diatraea saccharalis* (F.) (Lepidoptera, Crambidae) and *Castnia licoides* Boisd. (Lepidoptera, Castniidae) (Blackburn, 1950). However James (1946) found that drift dusting with gamma BHC and DDT for control of *Aeneolamia flavilatera* in Guyana had no apparent effect on the incidence of other insect pests. More recently, Fewkes and Buxo (1966d) found a generally lower level of small (*Diatraea saccharalis* (F.), *D. impersonatella* (Wlk.) and *D. centrella* (Mösch.)) and large (*Castnia licoides* Boisd.) moth borer damage in fields sprayed from the air with carbaryl, carbophenothion or phorate for frog hopper control, than in unsprayed fields.

In insecticide trials, assessment of the various treatments is generally made by comparison of frog hopper populations in treated and untreated plots. Most trials are concerned either with nymph or adult control, according to the method of treatment, and only the appropriate stage may be sampled. In small plot trials, adult counts are of limited value, as migration between plots tends to obscure the treatment effects. Frog hopper nymphs (*A. varia* subsp.) have long been known to occur both above and below ground (Williams, 1921) but most workers have assessed nymph infestations by above-ground counts only.

In an early trial with cyanogas for frog hopper nymph control, Follett-Smith (1926) assigned a series of 'marks' to nymph infestations in a number of randomly selected stools in each plot. The heaviest infestations, gauged visually by the amount of frog hopper spittle present, were marked '5', and the lowest (no spittle) were marked '0'. The 'percentage intensity of infestation' was calculated by expressing the sum total of marks in each plot as a percentage of 5 times the number of stools examined. After treatment the infestations in the same stools were re-assessed, and the 'percentage destruction' estimated $((A - B)/A \times 100)$, where A = percentage intensity before, and B = percentage intensity after treatment. Everly (1958) found that visual ratings of meadow spittlebug (*Philaenus leucophthalmus* (L.)) infestations did not give an accurate estimate of high populations. However, he considered that this sampling method was adequate for screening insecticides.

Most other authors have made direct counts of frog hopper nymphs present above ground in a number of cane stools in each plot. The cane stool has generally been used as a sampling unit for nymph populations, without regard to variation in its size (Blackburn, 1949; Potter and Carrington, 1949; Little, 1953; Neate, 1958; Merry *et al.*, 1963). However, Fewkes (1961b) showed that there is generally

a positive linear relationship between the number of nymphs per stool and stool size, as measured by the number of stems per stool. This relationship applies to both above ground and total nymph populations and may account, on average, for about 50% of the sampling variance on any one date. Adjustment of the counts to a standard sampling unit (e.g. nymphs per 10 stems) may therefore considerably reduce the error variance, improving the precision of statistical comparisons between treatments. This procedure has been adopted by some (Fewkes and Buxo, 1965a; Fewkes and Lawrie, 1967). They found the variance of the adjusted counts to be unstable, and recommended their logarithmic transformation prior to statistical analysis. They also emphasized that valid assessments of the residual activity of treatments can only be made for the periods when the nymph populations in control plots are rising.

Sampling of adult frog hopper populations is simple when adults (e.g. those of *Aeneolamia varia* subsp.) have the habit of congregating in the funnels (upper leaf axils) of sugar cane during the day. A cane stem can be grasped just above the base of the funnel and the adults counted as the leaves are released one by one (Fewkes, 1961a). All the stems in a stool may be sampled in this way. However, it is preferable to take a series of stems from different stools in order to avoid undue disturbance of the insects. Because of migration it is inadvisable to attempt the assessment of adult populations in areas less than about half an acre. For aerial spraying trials, plots of 2-6 acres have been used (Fewkes and Buxo, 1965b).

Assessment of the ultimate results of insecticide treatments requires comparative studies of population trends of the pest species and its natural enemies, in treated and untreated areas, over an extended period. In insecticide trials in Trinidad, the best treatments, e.g. carbophenothion at 6 lb/acre (2% dust) and toxaphene at 20 lb/acre (6.7% dust), rarely persist to give control of more than two broods of frog hoppers, re-infestation occurring by migration from untreated plots (Fewkes and Buxo, 1965a). This is borne out by the results of applications of these treatments on a field scale. The insecticides undoubtedly have some effect on natural control factors and on other insects, but this has not been carefully studied. Despite the heavy mortalities inflicted upon sugar cane frog hopper populations in Trinidad every year, there is no evidence that the incidence of the pest has declined. Migration from untreated areas and the immunity of diapausing eggs to the treatments apparently ensure that there is a carry-over from year to year, sufficient to maintain heavy infestations of the pest. The method presently employed, treating frog hopper infestations on an individual field basis, rather than in large, continuous areas, probably enhances this situation.

Where feasible, chemical control of sugar cane frog hoppers should be timed to minimize its effect on their natural enemies, and, if possible, selective insecticides non-toxic to beneficial insects and wild life, should be used. In this respect, the overall biological effect of insecticidal treatments applied for frog hopper control over large unit areas needs careful study.

3. Cultural Control

Williams (1921) suggested several changes in cultivation practices that would be likely to make sugar cane plantations less suitable habitats for the development of frog hopper populations. These included soil improvement by manuring, tillage and the provision of adequate drainage, the reduction of ratooning, the rotation of other crops with sugar cane, and the planting of varieties resistant to frog hopper attack.

There is no doubt that sugar cane growing in badly drained, compacted, infertile soil, is more susceptible to frog hopper attacks than healthy cane. However, there is no indication that any improvements in the manuring, tillage or drainage of sugar cane fields, can prevent frog hopper attacks and the development of blight, or make conditions unfavourable for this pest (Pickles, 1942). The cultivation of the crop, in these respects, has improved greatly in Trinidad over the last 40 years, but frog hopper continues to be a major pest. The reduction of ratooning might well help to make sugar cane fields a less suitable habitat for frog hoppers, because ploughing and re-planting a field practically eliminates the resident frog hopper population (Pickles, 1933*b*). However the cultivation of plant canes only is impracticable from an economic standpoint. Since 1950 there has been a tendency to take as many ratoons as possible, as it is cheaper to control frog hopper with insecticides than to plough and replant fields frequently (Blackburn, 1954).

Williams (1921) suggested that legumes, yams or sweet potatoes might be grown in rotation with sugar cane, in order to improve soil conditions and reduce frog hopper infestations. The advantage of this system with regard to frog hopper control is that every year some part of the cultivated area would offer an unsuitable environment for the insect. With good management, some areas could be maintained virtually free from frog hopper attack. However, in those areas where frog hoppers are pests, rotation of sugar cane with other crops is not generally practised, continuous cultivation of sugar cane being more profitable.

Field observations have indicated that some sugar cane varieties are less susceptible to frog hopper attack than others (Williams, 1921; Steven and Potter, 1928; Taylor and Pickles, 1934; Pickles, 1942). Fennah (1939) indicated a possible physiological basis for these differences when he found that adult frog hoppers were more attracted by the leaf odour of a susceptible variety (B.H.10/12) than by that of a resistant variety (Co. 213). Such a mechanism of resistance could only be operative when the insect has a choice of varieties, and in commercial plantations there may be little or no choice. A serious attempt to select varieties that are truly resistant to frog hopper damage, or that are physiologically less suitable for the development of frog hoppers, would be well worthwhile. The latter approach might be explored by determining the rate of development and reproductive capacity of frog hoppers reared on different varieties. Any differences might be correlated with a particular parental stock, or possibly with a particular biochemical

characteristic. Attempts to incorporate genes, which may regulate the production of chemical resistance factors, from 'tolerant' native grasses into new sugar cane varieties, as suggested by Vlitos (1962), might also yield useful results.

Briton-Jones (1927a) suggested flooding sugar cane fields at a critical period in the life history of the frog hopper to force the nymphs above ground, where they might perish or be destroyed by insecticides. This was tried in Guyana for the control of nymphs of *Aeneolamia flavilatera flavilatera* (Urich) (Pickles, 1945; James 1946). The addition of a film of oil to the flood water caused a high nymphal mortality. However, outbreaks of frog hoppers occurred soon after the water was drained off, perhaps because the flooding stimulated hatching of eggs present in the soil or made the soil more attractive to *A. flavilatera flavilatera* females for oviposition.

4. Biological Control

Detailed studies of the natural enemies of sugar cane frog hoppers have been made only in Trinidad (Urich, 1915; Williams, 1921; Pickles, 1933a). Pickles (1933a) considered that the most important natural enemies of *Aeneolamia varia saccharina* were various egg parasites, particularly *Anagrus urichi* Pickles (Hymenoptera, Mymaridae), a predator of the nymphs, *Salpingogaster nigra* Schiner (Diptera, Syrphidae), and the 'green muscardine' fungus, *Metarrhizium anisopliae* (Metch.) (Entomophthoraceae), which attacks the adults.

Rorer (1910, 1911, 1913) developed a method for mass-producing spores of the green muscardine fungus. Inoculation of frog hopper infested fields with the spores resulted in the death of many frog hopper adults and some nymphs. Briton-Jones (1927b) found that although, under suitably humid weather conditions, artificial infection with spores of the green muscardine fungus could induce epidemics of the disease in the field, insufficient frog hoppers were destroyed for practical purposes. Kershaw (1913) recommended that an attempt should be made to rear the Syrphid fly (*Salpingogaster nigra*) in captivity during the dry season, so that large numbers of this predator could be released early in the wet season when it is relatively scarce, probably due to its inability to survive in sugar cane areas throughout the dry season. Despite the efforts of Guppy (1913, 1914), mass rearing of the Syrphid did not prove feasible, and the work was abandoned in 1915. Jones and Potter (1929) suggested that 'covers' should be provided for birds, many of which feed on adult frog hoppers, by planting small groups of trees amongst the cane fields. This was done in some areas but unfortunately, no studies have been made of the effect of birds on sugar cane frog hopper populations.

The first attempt to establish biological control of a sugar cane frog hopper (*Aeneolamia varia saccharina*) by the introduction of a natural enemy was made in 1911, when the 'Mexican bug', *Castolus plagiaticollis* Stål (Hemiptera, Redu-

viidae), was introduced into Trinidad from Vera Cruz, Mexico. It failed to survive when liberated (Urich, 1914b). A further introduction of the Mexican bug into Trinidad in 1958 also proved unsuccessful (F.B. Little, *in litt.*) although, in laboratory cages, it fed readily on froghopper adults.

In 1916, when *Aeneolamia varia saccharina* had become a major sugar cane pest in Trinidad, a search for froghopper parasites that might be suitable for introduction into Trinidad was made in nearby countries (Williams, 1921). It was terminated in 1917 after visits to Guyana, Surinam, Venezuela, Canal Zone, Panama, Colombia, Martinique and St. Lucia, failed to reveal any natural enemies of froghoppers essentially different from those already found in Trinidad. Further explorations in the West Indies, Guyana, Surinam, Venezuela, Colombia, Panama, Costa Rica and the Lower Amazon Valley, during the period 1928 to 1935, had the same result (Pickles, 1942).

More recently, a study of the natural enemies of froghoppers in East Africa, particularly Uganda, was started (Fewkes and Buxo, 1965a). Froghoppers of the genus *Locris* (Cercopidae) have been found to be attacked by a Mymarid egg parasite and by a Syrphid, *Asarcina ericetorum albifacies* Bezzi, which feeds on the nymphs. Adult froghoppers of the genera *Poophilus*, *Cordia* and *Clovio* (Aphrophoridae) are commonly parasitized by *Halictophagus* sp. (Strepsiptera). One or more of these insects may be useful in the biological control of sugar cane froghoppers. The natural enemies of *Locris* spp. are the most likely to be suitable, as the genus *Locris* is more nearly related to the genera with economically important sugar cane froghoppers (family Cercopidae), than are *Poophilus*, *Cordia* and *Clovio* (family Aphrophoridae).

5. Summary

Several indigenous species of froghoppers are important pests of sugar cane in Trinidad and in South and Central America. Yield losses in sugar cane attacked by these pests commonly exceed 1 ton sugar/acre. The main methods of control involve the use of insecticides. There have also been attempts to achieve cultural and biological control.

The life cycle of sugar cane froghoppers takes about 2 months and the annual number of generations is governed largely by weather, there being 2 to 4 broods according to the duration of the rainy season. Some species survive the dry season as diapausing eggs in the cane field soil. Elimination of the first brood (after the dry season) in all infested fields should theoretically prevent the occurrence of further broods, but this has not been practicable, and re-infestation of fields treated with insecticide takes place by migration of froghoppers from untreated areas.

Control of nymphs is achieved by the application of insecticidal dusts to the bases of sugar cane stools, where the nymphs feed on the roots. Adults are

controlled by application of insecticides to the cane foliage, on which they feed, by drifting dusts over sugar cane fields in calm conditions (usually at night), or by aerial spraying.

For effective nymph control, insecticides having prolonged residual activity are required. The most successful of these have been *gamma* BHC, carbophenothion, dieldrin, phorate and toxaphene. Carbaryl, DDT, endosulfan and isobenzan have also been used. Resistance of frog hopper nymphs to *gamma* BHC and to other organochlorine insecticides has been reported from Trinidad. This resistance is apparently unstable, tending to disappear when organochlorine insecticides are replaced by organophosphate and carbamate insecticides.

Both *gamma* BHC and DDT dusts, applied by drift dusting or from the air, have been used for adult frog hopper control. In trials, better results have been obtained with foliar sprays of carbaryl and imidan. Aerial applications of these, or other suitable sprays, may serve to restrict the development of heavy frog hopper infestations, provided the areas treated are large and continuous enough to avoid re-infestation by adult migration. The timing of the applications would be critical, and rigorous control of the first brood should be the objective.

The efficacy of chemical control methods for sugar cane frog hoppers has so far been assessed by the immediate benefits obtained, such as the prevention of blight in the year of treatment. There is no indication that the methods used have caused a decline in sugar cane frog hopper incidence over a period of several years. This is probably due to re-infestation of treated fields by migration, and to the immunity of diapausing eggs to the treatments. Future control measures should be aimed at preventing the carry-over of frog hopper infestations from one year to the next, as well as ensuring short-term prevention of blight.

Some measure of cultural control of sugar cane frog hoppers could probably be achieved by growing fewer ratoon crops and by the rotation of other crops with sugar cane. However, it appears to be more profitable to practise chemical control of frog hoppers and grow sugar cane continuously with as many ratoon crops as possible. The selection of varieties resistant to frog hopper attack seems the most acceptable approach to cultural control.

Biological control, by augmenting the number of species of natural enemies of frog hoppers present in an environment, has not been possible. An attempt to establish in Trinidad an insect predator of frog hoppers from Mexico was unsuccessful. This approach, however, seems more likely to succeed than the breeding and release of indigenous species. Searches in the Neotropical region have not revealed any natural enemies essentially different from those found in areas where frog hoppers are pests of sugar cane. Studies of the natural enemies of African frog hoppers seem to hold rather more promise for the discovery of species suitable for the biological control of sugar cane frog hoppers.

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Mixed Risk-Spreading Strategies and the Population Dynamics of a Brazilian Pasture Pest, *Deois flavopicta* (Homoptera: Cercopidae)

ELIANA G. FONTES, CARMEN S. S. PIRES, AND EDISON R. SUJII

Empresa Brasileira de Pesquisa Agropecuária, Centro Nacional de Recursos Genéticos e Biotecnologia, C.P. 02372, Brasília, DF, 70.849-970, Brazil

J. Econ. Entomol. 88(5): 1256-1262 (1995)

ABSTRACT *Deois flavopicta* (Stål) is a predominant species of grass-feeding spittlebug in Central Brazil. The climate in this region is a humid/dry cycle with year-long mild temperatures. We investigated the population dynamics, diapause, and voltinism of this insect. *D. flavopicta* has 3 population peaks during the rainy season, and it diapauses in the egg stage during the dry season. The proportion of offspring entering diapause varies, with few or no diapausing eggs in the beginning of the rainy season and up to 100% eggs in diapause by the season end. Diapausing eggs hatched in 61–360 d. Fifty-two percent of the eggs, however, end diapause in September and October, the most probable period for the 1st heavy rains of the season. High local populations of *D. flavopicta* may severely damage a host plant, making it unsuitable for the development of future generations of the insect. Apparently, this species migrates to other feeding sites when faced with low nutritional quality food.

KEY WORDS spittlebug, bet hedging, diapause, voltinism

FIVE SPECIES OF pasture spittlebugs (Homoptera, Auchenorrhyncha: Cercopidae) are important pests of grasses in >150 million ha of cultivated pastures in Brazil. Pasture spittlebugs cause significant reductions in cattle-stocking densities and consequent negative effect on meat and milk production (Menezes 1982). These species are endemic and feed on native and introduced grasses (Menezes 1982). *Deois flavopicta* (Stål) and *Zulia entreriana* (Berg) are the most important pests in regions where a high percentage (57%) of the bovine herds are located (Scolari 1988). *Deois shack* (F.), *Deois incompleta* (Walker), and *Aeneolamia selecta* (Walker) are important in the Amazon and Northeast region of Brazil.

Because of the predominance of *D. flavopicta* in the states of São Paulo, Minas Gerais, and Goiás, which together form the main meat and milk production region, this species is considered the most serious pasture pest in Brazil. In the Federal District of Brazil (Brasília), where this study was conducted, *D. flavopicta* represents 97% of the total spittlebug population in pastures (Sá 1981). Despite the economic importance of *D. flavopicta*, there are no efficient, widely adopted control strategies for this pest.

The life cycle of *D. flavopicta* was studied in the states of São Paulo (Pacheco 1981, Milanez et al. 1983), Minas Gerais (Melo et al. 1984), and Mato Grosso do Sul (Valério and Oliveira 1982). However, the implementation of an integrated pest management program for this pest requires more

detailed information on the biotic and abiotic factors, which influence the population dynamics of this insect.

Deois flavopicta heavily attacks cultivated pastures of *Brachiaria decumbens* Stapf (Gramineae) in the phytogeographic region of Central Brazil, called cerrado. This area has soils low in fertility and high in aluminum toxicity. *B. decumbens* was successful in colonizing these poor soils, growing aggressively, and demanding low input and little management. For this reason this grass is now cultivated in >80% of the pastures in Central Brazil, where 42% of the Brazilian bovine herds are raised (Scolari 1988). *B. decumbens*, however, is very susceptible to attack by *D. flavopicta*, which moved from the native and naturalized grass hosts to this newly introduced species (Menezes 1982).

Nymphs of *D. flavopicta* suck the sap and debilitate the plant; however, most damage is caused by the adults. Valério and Nakano (1987, 1988) showed that *Z. entreriana*, a species that is closely related to and co-occurs with *D. flavopicta*, feeds on the xylem, injects salivary secretions, and causes phytotoxemia. The leaves dry out at the tip and eventually die. We have observed similar damage by *D. flavopicta*, and as with many other cercopid species (Valério and Nakano 1987, 1988), *D. flavopicta* also may feed in the xylem and inject salivary secretions.

During the dry months of the year (June through August), when low humidity and lack of food plants prevent survival of the insect to active

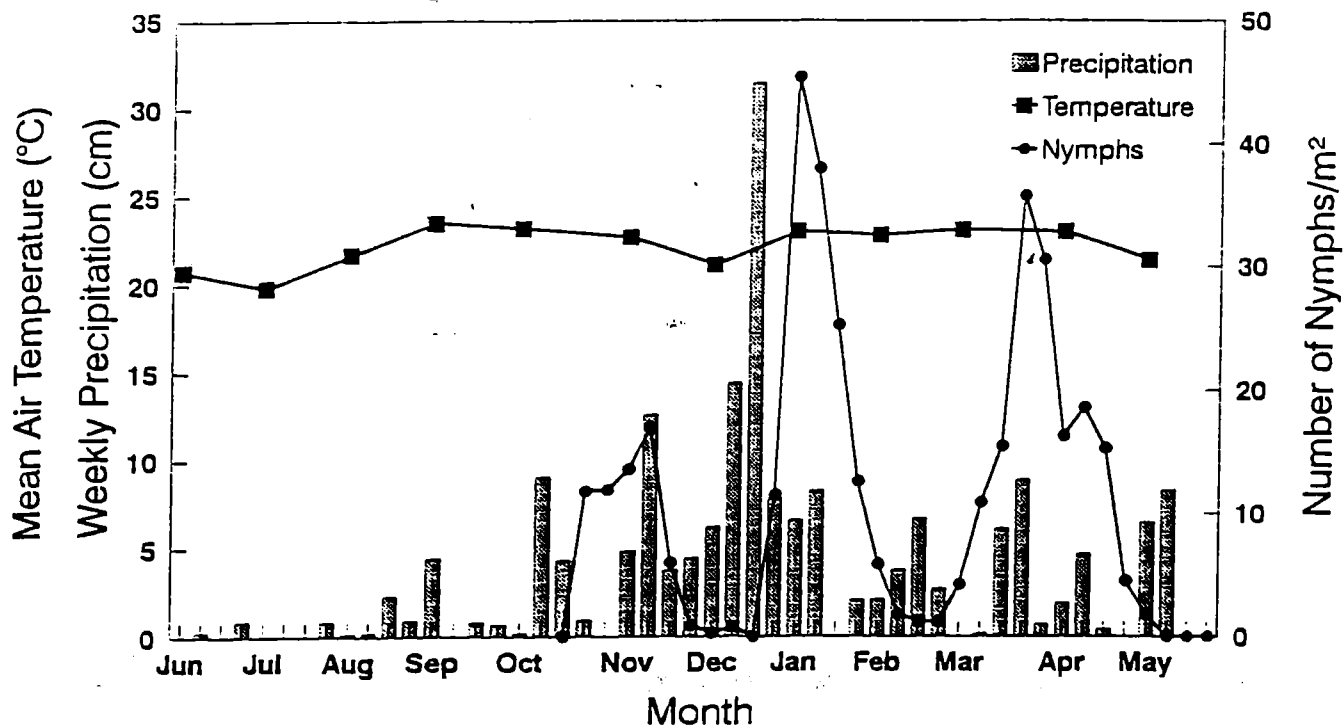


Fig. 1. Average monthly temperature, average weekly precipitation (1973–1993), and population fluctuation of *D. flavopicta* nymphs (1989–1990) in the Federal District of Brazil.

stages. *D. flavopicta* persists in the form of diapausing eggs in the soil. Diapause promotes the synchronization of the annual life cycle with the arrival of the rainy season. Our objective in this work has been to understand insect voltinism and phenological cycles in cultivated pastures in relation to the weather and to the food quality and supply. Here we describe the mechanisms and discuss the adaptive importance of insect egg diapause. The results contribute to a better understanding of the adaptive mechanisms for the growth and survival of this species and will support the development of more efficient control methodologies.

Material and Methods

Study Sites. This research was conducted in 3 areas ≈ 40 km north of Brasília (DF), in Planaltina District ($15^{\circ} 35' \text{ L}$, $47^{\circ} 42' \text{ W}$; 1,000 m altitude). June and July are the coldest months, with an average air temperature in the last 20 yr of 19.9 and 19.0°C, respectively. The warmer months are September and October, with an average air temperature of 22.9 and 23.0°C, respectively (Fig. 1). There are 2 well-defined seasons in the year: rainy, from September–October through April–May, and dry, during the other months.

One of the experimental areas (site 1) was at the experimental fields of Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)/Centro Nacional de Pesquisa Agropecuária dos Cerrados (CPAC), and the other 2 (sites 2 and 3) were located in pasture fields of an Agricultural School (Colégio Agrícola de Brasília). The rainy season in Central

Brazil (October through May) is also called the agricultural year, when crops are grown. In agricultural year 1986–1987, the studies were done only at site 2. From 1987–1988 to 1989–1990, experiments were done in 2 areas, sites 1 and 2, which were separated from each other by ≈ 5 km. The objective was to compare the performance of 2 different *D. flavopicta* populations. In 1990–1991 and 1991–1992, the studies were conducted only at site 3.

The 3 experimental areas (50 by 50 m) were cultivated with *B. decumbens*. The pastures in sites 1 and 2 were newly planted (≈ 3 yr old). Site 3 was an old pasture (≈ 10 yr old) that had been exposed to extensive cattle feeding.

Population Dynamics. Nymphs and adults were sampled from October to May, when the insect is common in the field. Twelve equally spaced compass directions were marked, starting from the center of the area. Three directions were selected at random each collecting day to sample adults and nymphs. Nymphs were sampled for 3 yr, from 1989–1990 through 1991–1992. One quadrat (1 by 1 m) was sampled for nymphs in each of the selected directions, counting every individual present in the area. The position of the sampled quadrat in each of the 3 directions was chosen by randomly picking a number and walking that number of steps starting from the center of the area. Adults were sampled during agricultural years 1986–1987 through 1991–1992 by sweeping with an insect net from the center to the edge, following the 3 directions. Captured adults were taken to the laboratory to be counted and to determine sex.

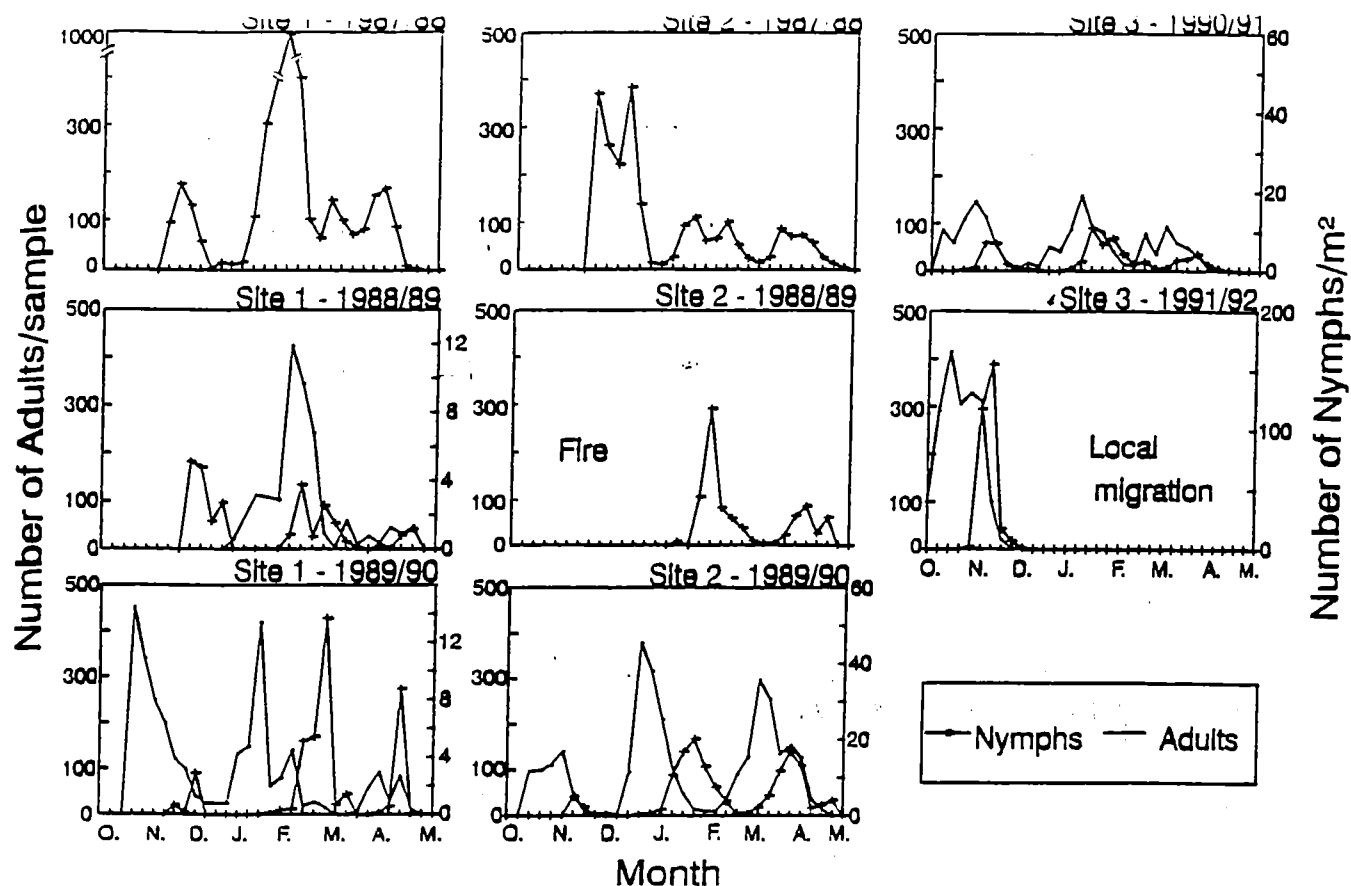


Fig. 2. Population dynamics of *D. flavopicta* in 3 sites (1–3) from 1987 through 1992. Fire indicates the absence of 1st generation in a site that was burned near the end of the dry season. Local migration shows the local extinction of a high population grown on a poor food quality site.

environmental conditions. The females collected in our studies during the 1st-generation peak, and maintained in field cages or taken to the laboratory for oviposition, probably were young individuals that had not yet obtained sufficient nutrients for ovary maturation. Nilakhe (1985) reported the migration of spittlebugs from pastures to rice fields in the state of Mato Grosso do Sul. Approximately 80% of the observed migratory individuals were *D. flavopicta*, and 20% were *Z. enteriana*, although this last species is more abundant in that state. Other evidences of short-range movements of *D.*

flavopicta are given by Nilakhe and Buainain (1988).

Phenology of *D. flavopicta*. Eggs incubated under favorable conditions in the laboratory show 2 distinct developmental patterns: a fast development pattern that takes 16.3 ± 3.27 d (mean $\pm$ SD) ($n = 98$) to hatch (Fig. 3), and a diapause pattern that may take from 61 to 360 d to hatch (Fig. 3). As shown in Fig. 4, females from the 1st generation lay a high percentage of fast-developing eggs. Second-generation females lay a mix of fast-developing and diapausing eggs. This transition from nondiapause to diapause eggs normally occurs in January. Early emerging females of the 2nd generation lay a small proportion of diapausing eggs. The proportion of eggs diapausing increases gradually with the later-emerging females, reaching up to 100% near the end of the 2nd peak and during the 3rd peak (Fig. 4). A higher proportion of diapausing eggs is produced in late January, February, March, and April. When the 2nd generation was delayed until February and March, as in site 1, 1989–1990 (Fig. 4), the regular transition from nondiapause to diapause was not observed.

Variation in the seasonal pattern of diapause may occur. In the year 1987–1988, $\approx 40\%$ of diapause eggs were observed among the brood of the 1st-generation populations inhabiting both site 1 and 2. This is an indication that female parents

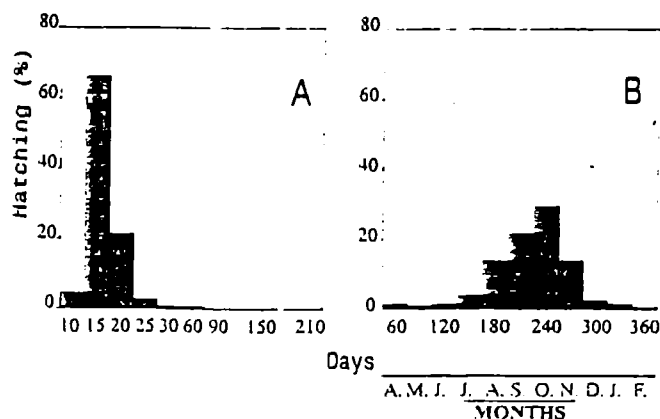


Fig. 3. Hatching distribution of fast developing (A) and diapause (B) eggs of *D. flavopicta*.

Results and Discussion

In 1991–1992, adults of the 1st generation were collected and placed in field cages to lay eggs. The cages consisted of an iron structure with a 0.4-m² base, 0.8-m high, covered by a white plastic net, with an open bottom. These cages were placed over grass plants with the base touching the ground. Adults collected in the nearby fields were placed in the cages through a lateral opening containing a zipper. After the death of the insects, the surface layer of the soil under each cage was collected, taken to the laboratory, and searched for *D. flavopicta* eggs. Ovary development in this population was estimated by randomly collecting 20 females in the field and dissecting in the laboratory; 2 times corresponding with peak adult abundance.

Measurements of air and soil (2 cm deep) temperature, relative humidity, and rainfall during the study period were obtained from an agrometeorological station located at EMBRAPA/CPAC, within ≈7 km of the study sites. The instrumentation used to obtain the measurements are an Isez Quartz Precision Thermo-hygrograph (Isez Seisakusho), Earth Thermograph (Ota Keiki Seisakusho), and Pluviometer (Lambercht). Data in this station are collected once a day.

Hatching Pattern of Nondiapausing and Diapausing Eggs of *D. flavopicta*. To follow the embryonic development of nondiapausing and diapausing eggs of *D. flavopicta* during the 6 yr of this study, adults were collected from the field weekly, returned to the laboratory, and placed in round plastic cages 0.2 m in diameter and 0.3 m high with bottoms open. The cages were placed on trays containing a layer of agar, in which the females laid eggs. As food for the insects, a small bottle containing several young stalks of *B. decumbens* was placed in the center or hung from the edge of the cage. Each cage received 50 pairs of spittlebugs. After 3 d, the eggs were collected from the agar with the aid of a needle.

The eggs were incubated in plastic petri dishes containing a layer of cotton at the bottom covered with filter paper on which the eggs were placed. This layer was kept saturated with distilled water, such that the eggs were permanently exposed to 100% humidity. Each week, 5 dishes containing 50 eggs each were prepared. The dishes were maintained at 28°C in a glass door Percival incubator, which allowed natural light (photoperiod was variable throughout the experimental period from 12 to 14 h light). The number of newly hatched eggs was observed every 2–3 d for several months until complete development or death of all the eggs. The duration of embryo development was used to estimate the percentage of nondiapausing and diapausing eggs in each generation, and to establish the duration of diapause. We predicted development would resume as soon as diapause ended because favorable developmental conditions prevailed.

Population Dynamics. In the Federal District of Brasília, *D. flavopicta* produces 3 population peaks, although temporal variations may change this general pattern in a given area and year (Fig. 1). The size and timing of *D. flavopicta* population peaks vary from year to year in relation to the annual rainy season (Fig. 1), which is also the period of greatest food availability and higher temperatures (Fig. 1). The size and timing of each generation also varies among nearby locations in a given year (Fig. 2, site 1, 1989–1990 and site 2, 1989–1990).

The profile of *D. flavopicta* population dynamics in different years and locations (Fig. 2) indicates an adaptive plasticity of this insect to survive in a variable environment. Two or 3 generations a year of this insect have been observed in other regions (Reis et al. 1980, Pacheco 1981, Melo et al. 1984, Koller 1992). During the 6 yr of our studies, the length of the life cycle of *D. flavopicta* varied from year to year, but a clear variation on its voltinism has not been observed. In 1988–1989, the occurrence of fire in site 2 eliminated the 1st generation of *D. flavopicta* but the field was reinfested, resulting in the occurrence of a 2nd and 3rd generation (Fig. 2). Dispersing insects from the nearby fields probably recolonized the area.

A variation in the regular profile of *D. flavopicta* dynamics also was observed in site 2, 1987–1988, and site 3, 1991–1992 (Fig. 2). The high number of individuals in the 1st population peak (almost 2-fold higher than the highest population observed at sites 2 and 3) resulted in considerable feeding-induced toxic burn of the grass, making it unsuitable for development of the following generations. During December and January of 1991–1992, when the 2nd peak of nymphs and adults, respectively, should appear, the weather generally was favorable for *D. flavopicta*. A cumulative precipitation of 639.6 mm was registered and the average soil temperature at 2 cm deep was 25°C. Despite that, field collected females of the 1st generation did not lay eggs in the laboratory, although the same experimental methodology adopted in former years was used. Likewise, females collected and kept in field cages did not lay eggs. Eighty percent of the females collected in the field and dissected in the laboratory did not have developed ovaries.

It appears that the pasture nutritional quality was the determining factor in preventing the occurrence of 2nd and 3rd generations in site 3, 1991–1992. It is possible that the pasture, being old (≈10 yr old), without adequate management, and heavily damaged by the 1st generation of pasture spittlebugs, had become nutritionally inadequate for good performance of the following generations. We suggest that adults of the 1st generation of year 1991–1992 soon after emerging mi-

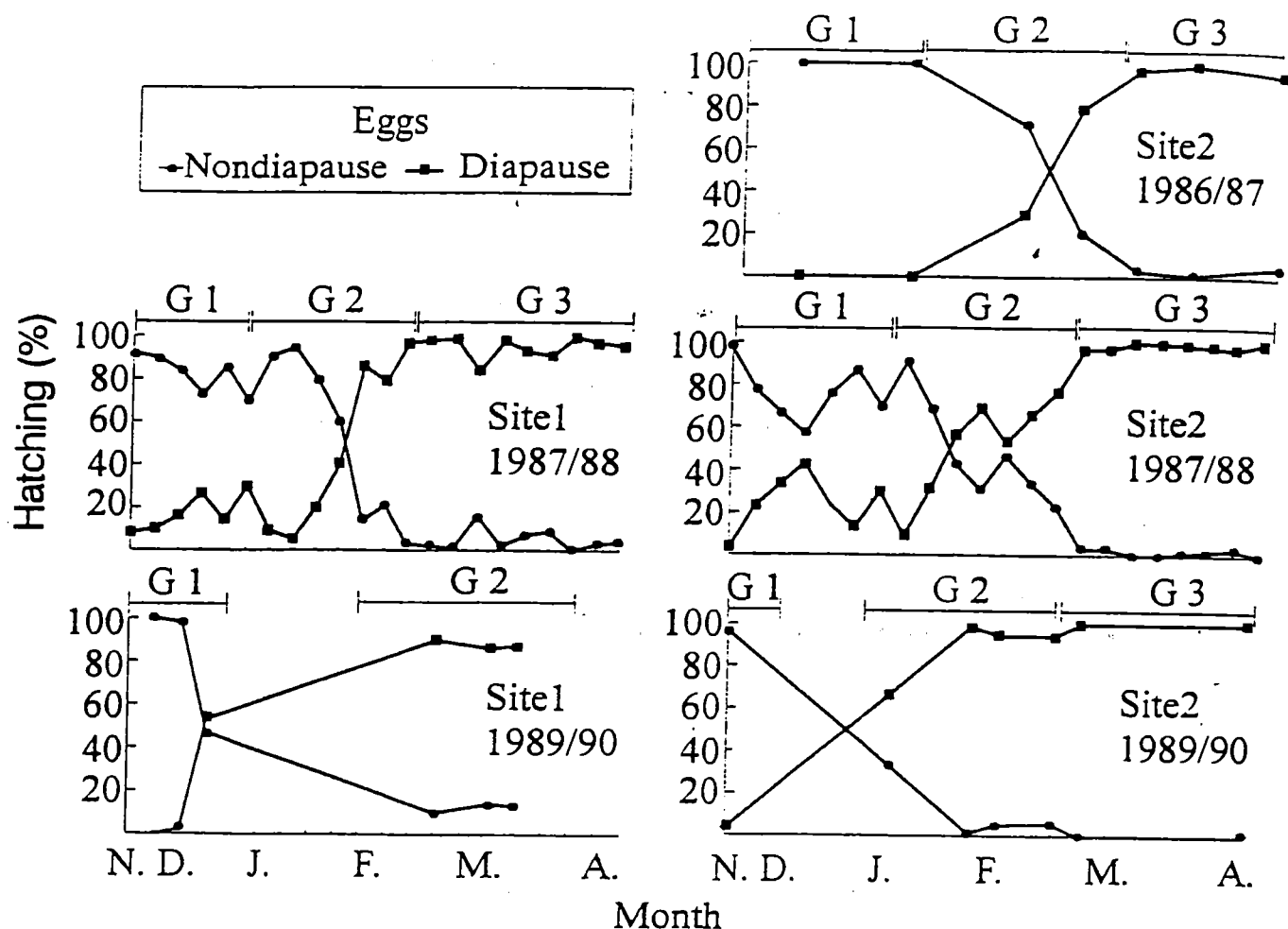


Fig. 4. Percentage of nondiapausing and diapausing eggs laid by each generation of *D. flavopicta*. G1, G2, and G3 represent 1st, 2nd, and 3rd generation, respectively.

may control diapause expression in their offspring according to environmental cues. This variation in the proportion of eggs in diapause appears to be a bet-hedging strategy adopted by *D. flavopicta*. Bet hedging is a risk-spreading strategy associated to temporal heterogeneity in the environment (Cohen 1966).

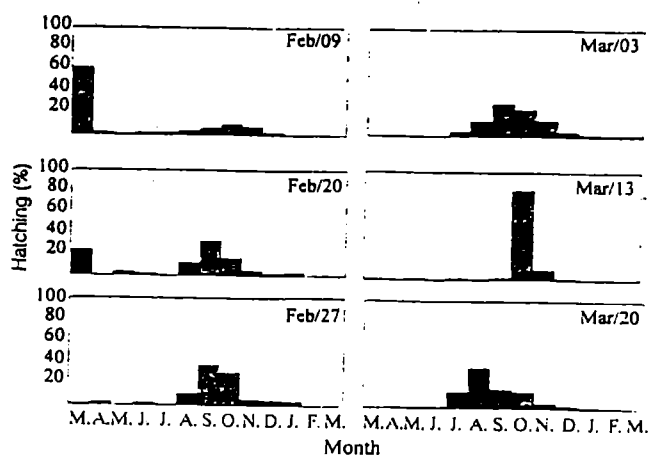


Fig. 5. Hatching pattern of *D. flavopicta* eggs from different oviposition dates during 2nd (February) and 3rd (March) generations.

Diapausing eggs of a particular field population and from different oviposition dates have diapause programmed for different durations, presenting a variation amplitude from 61 to 360 d (Fig. 5). On average, however, 80% of the eggs hatch between August and November. But most hatching (52%) occurs between September and October (Fig. 3). This hatching variation probably represents another bet-hedging strategy adopted by *D. flavopicta* in its reproductive allocation, with the majority of the eggs programmed to end diapause during the most probable period of 1st heavy rains of the season.

With a gradual increase in the fraction of offspring entering diapause and varying the degree of diapause among a family of progeny to promote hatching variation, *D. flavopicta* is adopting a double risk-spreading strategy by diversifying its offspring. As discussed by Bradford and Roff (1993), this strategy may be favored by natural selection because at least part of the offspring will be adapted to the unknown future environment. A gradual transition from nondiapausing to diapausing eggs has been demonstrated experimentally in other insects, such as the mosquito *Wyeomyia smithii* (Coquillett) (Istock 1981) and the crickets *Grillus fir-*

mus Scudder (Walker 1980) and *Allonemobius fasciatus* (De Geer) (Bradford and Roff 1993). Variance in hatching times also was demonstrated in *C. firmus* (Walker 1980) and in the mosquito *Aedes caspius dorsalis* Meigen (Khelevin 1958).

In the tropics, well-defined periods of heavy rains allow for periodic flushes of new vegetation and an abundance of organic matter that favor the evolution of seasonality (Delinger 1986). *D. flavopicta* voltinism is regulated by the length of the rainy season, which, in Central Brazil, in years of typical weather, lasts 8 mo. Shorter or longer rainy periods, however, may occur. Very short periods of drought in the middle of the rainy season are common. Roff (1983) suggests that natural selection favors evolutionary mechanisms that allow the organism to vary the length of its generations according to conditions found during a given year and within a region. In *D. flavopicta*, natural selection favored the evolution of a mixture of risk-spreading strategies that allows for shaping the life cycle to the variable conditions that may be experienced in different years and localities.

A mixture of proportional diapause and hatching variation may have evolved along the phylogenetic line of *D. flavopicta*. The life cycle of other tropical grass-feeding spittlebugs in Brazil, *Z. entreriana*, *D. incompleta*, and *D. schacki*; Trinidad, *Aeneolamia varia saccharina* (Dist.); and Mexico, *Aeneolamia occidentalis* (Walker) and *Prosapia similans* (Walker) are also highly synchronized with the rains, promoted by egg dormancy (King 1975, Oomen 1975, Melo et al. 1984). *Z. entreriana* (Koller and Honer 1993) and *A. varia saccharina* (Fewkes 1963) lay eggs exhibiting widely different degrees of diapause. This allows hatch to continue during the dry season in those areas that remain favorable for development (Fewkes 1963).

The phenomenon of dormancy and other recurrent factors of the insect life cycle are little known in the tropics. Perhaps this is the reason why phenological studies have not received the attention they deserve in Brazil. However, these phenomena probably are very common. In *D. flavopicta*, for example, we observed diapause and migration, which will bring tremendous implications for the design of integrated pest management programs of this pest. It becomes evident that there is a need for more knowledge of the behavior, adaptive mechanisms, and survivorship strategies of pest insects. Such information would facilitate the design of accurate phenological models and the implementation of successful integrated management and biological control programs.

Acknowledgments

We acknowledge the field and laboratory work of the following students and technicians of the Ecology Laboratory at EMBRAPA/CENARGEN: Dagoberto F. Gomes, Denise Návila, João Sívio de O. Paes, Siranio J. Rocha, Sirayana de O. Ferreira, and William Sihler. We

thank Peter W. Price (Northern Arizona University) for helping with data interpretation and reviewing the manuscript, and Bonifácio Magalhães (EMBRAPA/CENARGEN), José R. P. Parra (University of São Paulo / ESALQ), and Bob O'Neil (Purdue University) for reviewing the manuscript.

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Received for publication 21 June 1994; accepted 13 March 1995.

EFFECTS OF SPITTLEBUG FEEDING ON FORAGE AND ROOT PRODUCTION OF *BRACHIARIA DECUMBENS* AND *BRACHIARIA BRIZANTHA* cv. MARANDU (BRA-000019)¹

GEORGE B. HEWITT²

ABSTRACT - The spittlebug *Zulia entreriana* was used in laboratory feeding tests to evaluate the degree of damage to the foliage and roots of *Brachiaria decumbens* and *Brachiaria brizantha*. Nymphal feeding on *B. decumbens* reduced the weight of foliage by an average of 21% and the roots by 36%; adults reduced the foliage weight by 27% and the roots by 48%. Nymphs and adults feeding on the same plant reduced the foliage weight by an average of 36% and the roots by 50%. The degree of damage was in direct proportion to insect density; the more insects per plant, the greater the amount of damage. In one test, significantly ($P < 0.05$) more new shoots were produced on *B. decumbens* plants that contained a high density of adults. The reduction in root weights due to insect feeding was about $1\frac{1}{2}$ time greater than that for foliage. *Brachiaria brizantha* was less affected by insect feeding than was *B. decumbens*. Weight differences between the control plants and the infested plants were less on *B. brizantha* and plant recovery, once insects were removed, was faster.

Index terms: *Zulia entreriana*, nymphal feeding, adults, insect, plant damage.

EFEITO DA ALIMENTAÇÃO DAS CIGARRINHAS-DAS-PASTAGENS NA PRODUÇÃO DE FORRAGEM E RAÍZES DE *BRACHIARIA DECUMBENS* E *BRACHIARIA BRIZANTHA* cv. MARANDU (BRA-000019)

RESUMO - A espécie de cigarrinha (*Zulia entreriana*) foi usada em teste de alimentação em laboratório com o objetivo de se avaliar o grau de dano na forragem e nas raízes de *Brachiaria decumbens* e *Brachiaria brizantha*. A alimentação das ninfas em *B. decumbens* reduziu o peso da forragem, em média, 21% e das raízes 36%; os adultos reduziram o peso da forragem em 27% e o das raízes em 48%. As ninfas e os adultos que se alimentaram da mesma planta reduziram, em média, o peso da forragem em 36%, e o das raízes, em 50%. O grau de dano foi diretamente proporcional à densidade dos insetos; quanto maior foi o número de insetos por planta, maior o dano. Num teste, a produção de brotos foi significativamente maior ($P < 0,05$) em plantas de *B. decumbens*, que continham alta densidade de adultos. A redução no peso das raízes, em consequência da alimentação dos insetos, foi cerca de $1\frac{1}{2}$ vez maior que a verificada na forragem. A *Brachiaria brizantha* foi menos influenciada pela alimentação desses insetos que a *B. decumbens*. As diferenças de peso entre as plantas-testemunhas e as infestadas foram menores em *B. brizantha*, e a recuperação da planta, após a remoção dos insetos, foi mais rápida.

Termos para indexação: *Zulia entreriana*, ninfas, adultos, insetos, alimentação, dano à pastagem.

INTRODUCTION

Some insect species have always been of economic concern on rangelands and pastures in many parts of the world. However, attempts at improving rangelands and pastures by introducing new plant species has often caused additional insect problems. For example, the introduction of the wheatgrasses into the western United States in the 1930's and 1940's has resulted in drastic population increases of black grass bugs which suck nutrients from the plants (Kamm & Fuxa 1977). Genung (1956) also reported the rapid expansion of

improved acreages in Florida, causing sucking insects to increase, and grass yield reductions, due to insect feeding, exceeding 50 percent.

This same situation is present in Brazil where two spittlebug species *Zulia entreriana* (Berg) and *Deois flavopicta* (Stål) have successfully adapted to extensive monocultures of introduced grasses of the genus *Brachiaria*. The effect of nymphal feeding is not readily visible but adult feeding results in streaking of leaves, leaf yellowing, and eventually in the browning of entire leaves. Both nymphs and adults occur during the rainy season (October-April) during the time of major forage production. When insect numbers are high, entire pastures can turn yellow or brown as a result of insect feeding. This type of damage has been observed for many years in central Brazil but there is only limited information

¹ Accepted for publication on August 4th, 1988.

² Eng. - Agr., M.Sc., USDA-ARS - Rangeland Insect Lab., Montana St. Univ., Bozeman, Mt. 59717 - USA.

on the actual amount of forage lost because of spittlebug feeding. Weaver & King (1954) and Everly (1959) reported on losses to alfalfa and red clover caused by spittlebug feeding in the United States. However, most research emphasis has been on the two-lined spittlebug, *Prosapia bicincta* (Say) which often causes severe damage to "Coastal" bermudagrass, *Cynodon dactylon* (L.) Pers. and other bermudagrass cultivars in the Southeastern U.S. (Beck 1963, Taliaferro et al. 1967, 1969). In Brazil the determination of the amount of damage resulting from spittlebug feeding has received limited attention and only in recent years (Silva 1982, Valério et al. 1982, and Valério 1985). This paper presents the results of laboratory feeding tests designed to evaluate the degree of plant damage caused by the spittlebug *Z. enteriana*. Forage and root reductions due to feeding by both nymphs and adults was determined for two grass species; *Brachiaria decumbens* Stapf., a species considered highly susceptible to spittlebug feeding and *Brachiaria brizantha* (Hochst ex A. Rich) Stapf. cv. Marandu (BRA-000019), a species reported to be resistant (Cosenza et al. 1983 and Nilakhe 1987).

MATERIAL AND METHODS

A total of eight tests where the spittlebug *Z. enteriana* was allowed to feed on plants were carried out in a greenhouse. In two tests (numbers 7 and 8) feeding damage to *B. decumbens* plants was compared to damage to *B. brizantha*. In the other six tests spittlebugs fed on *B. decumbens*. The amount of damage to the above ground portions of the plant and the roots was determined for small nymphs (Instars 1, 2 and 3), medium and large nymphs (Instars 4 and 5), adults, and nymphs and adults feeding together on the same plant. The number of days the insects remained on the plant, the age of the plants, and the number of times plant replicates were harvested following insect removal varied between tests. In test number 1, plants were grown in a nutrient solution, but in all other tests they were grown in soil. In test number six, ten days after the insects were removed from the plants the number of new shoots were counted in all treatments. Testing procedures were similar in all tests and can be described as follows:

1. Grass seeds were germinated in vermiculite and after 14 days were transferred to soil-filled plastic pots 9.5 cm in diameter; one seedling per pot.

2. When the plants were well established and at least 20 cm tall, they were assigned a number. A portable area meter was used to determine the leaf area of each plant and plants with leaf areas that varied greatly from the mean were discarded.

3. Plants were selected randomly for the various treatments. All treatments contained eight plants.

4. The plants to be used in a test were separated into two or more treatments. Each treatment contained enough plants to

allow plants to be harvested at intervals following the infestations.

5. Field collected nymphs and adults were used to infest the plants. Nymphs were placed at the base of the plants and observed to insure that they established on the plants. Adults were placed in circular cages of cheesecloth. The cages were secured to the top of the plastic pot with rubber bands and were supported 30 cm above the soil surface by a circular wire. The top was kept closed with a string. Nymphs and adults that died during the infestation period were replaced daily.

6. Plants were harvested at different times during the tests such as the midpoint of the infestation period, at the time the insects are removed from the plants, and at intervals following insect removal. Eight plants of each treatment were harvested at the selected times.

7. Harvesting consisted of removing the plant and soil from the plastic pot and then carefully washing the soil from the roots. The above ground part of the plant was then separated from the roots at the junction of the stem and root system. Both the roots and the above ground part of the plants were dried at 65°C for three days and then weighted.

8. The mean weight of the control plants was compared to the mean weight of plants in the infested treatments. Significance between treatments was determined by using Duncan's Multiple Range Test. The mean decreases in plant weights (% reduction) due to spittlebug feeding was also recorded each time the plants were harvested.

RESULTS AND DISCUSSION

All feeding treatments imposed upon the grass plants reduced foliage and root production as measured either at the time the insects were removed from the plants or at a time interval after insect removal. Weight reductions in both the foliage and roots resulting from adult spittlebug feeding were evident as early as three days after feeding had begun. In general root weights were reduced about 1¹/₂ time more than the above ground portion of the plant.

Within the eight tests, a total of 72 weight comparisons (36 for foliage and 36 for roots) were made between insect-free plants and infested plants of *B. decumbens*. For example, usually the first comparison of a test was made at the time the insects were removed from the plants and other comparisons were made at intervals (days) following insect removal. In only three of the 72 comparisons did the infested plants (either foliage or roots) weigh more than the control plants. Of the 72 comparisons, 46 were significantly ($P < 0.05$) different.

A total of 25 weight comparisons were made between insect-free plants and infested plants of *B. brizantha*. Six of these comparisons showed that the infested plant (either foliage or roots) weighted more than the control. Of the 25 comparisons only

ten were significantly ($P < 0.05$) different. Thus spittlebug feeding on *B. brizantha* had a lesser impact than on *B. decumbens*.

The reduction in plant weight (foliage and roots) due to different insect stage or feeding combinations is shown in Table 1. Forage reduction by adults was only slightly higher than that recorded for nymphs. Centro Internacional de Agricultura Tropical (1982) stated that adult damage is always more severe than nymphal damage even when the adult population is less than the nymphal population. The report estimated nymphal damage at 76.7% from 560 nymphs/1.25 m², adult damage at 83.7% from 39 adults/1.25 m², and damage from both nymphs (550/1.25 m²) and adults (81/1.25 m²) at 88.7%. However, in the tests reported on here the nymphs were allowed to feed for 16 days in test 1 and 20 days in test 2 compared to adults feeding for 3-7 days. The differences in time spent feeding by the two groups could account for the smaller differences in forage reduction. It appears that nymphal feeding adversely affects plant production even though the feeding effects are not readily visible. It is possible that nymphal feeding depletes the reserves in underground storage organs and photosynthesis assists in providing nutrients to the feeding nymphs that normally would result in plant growth. Beck (1963) reported that nymphal feeding severely damages Coastal bermudagrass in much the same manner as adults. He estimated damage to the foliage by different nymphal densities to range from 23 - 88%. Adults of *Protoparva bicincta* feeding on Coastal bermudagrass cause the leaves to become dry and brown similar to feeding damage by *Z. enteriana* and *D. flavopicta* in Brazil. Taliaferro et al. (1967) stated that reduction in root development in Coastal bermudagrass due to the feeding of *P. bicincta* adults is due primarily to cessation of photosynthesis and other necessary physiological processes, caused by the insect toxin turning the leaves brown and dry. However, in the tests reported on here the greatest reduction (36% for the foliage and 50% for the roots) in the weight of forage plants was due to a combination of nymphs and adults feeding on the same plant. A summary of the feeding on *B. decumbens* by both nymphs and adults is shown in Table 4.

Forage reduction (foliage and roots) to *B. decumbens* plants by different adult densities is shown in Table 2. Generally most workers have reported a higher degree of damage to plant foliage by adults than found in the present study. However,

in other studies the feeding period has been longer or the test densities higher. For example, Valério et al. (1982) in a greenhouse study measured the amount of regrowth (above 15 cm) after *Z. enteriana* adults at densities of 5, 10, and 20 had been feeding for twelve days. He reported the percent damage ranged from 70% at five adults/cage to 100% at 20 adults/cage. In a similar study carried out in the laboratory, Valério (1985) reported that reduction in plant growth above 25 cm ranged from 24% at two adults/cage to 91% at eight adults/cage after 45 days of feeding. Percent reduction on plant growth at the base of the plant up to 25 cm ranged from 12% at densities of two and four adults/cage to 36% at eight adults/cage. Valério (1985) also used in general the same experimental design under field conditions and found that forage reduction above 25 cm ranged from 34% at 25 adults/m² to 64% at 100 adults/m². Forage reduction from the plant base up to 25 cm ranged from 14% at 25 adults/m² to 17% at 100 adults/m². In this study, foliage reduction ranged from 11% at two adults/plant to 27% at 16 adults/plant.

The effect of spittlebug feeding on root production has received limited attention. Taliaferro et al. (1967) reported, based on greenhouse tests, that feeding damage to about 1/3 of the above ground plant material was sufficient to reduce root production and sod reserves by 50%. Valério (1985), from greenhouse tests found no significant root reduction after 45 or 90 days at densities of two and four adults/cage. However, at 8 adults/cage he reported a 52% reduction in root growth after 45 days and a 53% reduction after 90 days. In this study (Table 2) root reduction averaged 35% at two adults/plant and 52% at 16 adults/plant. However, adults were only on the plant for three days in one test and five days in another test.

Adult spittlebug feeding density also effected the number of new shoots arising from the base of *B. decumbens* plants. In test 6, counts were made of new shoots on 16 plants of each treatment ten days after the spittlebugs had been removed from the plants. The greater the insect density (feeding pressure), the greater the number of new shoots (Table 2). This would indicate that plant survival under intense feeding pressure may be at least in part dependent upon root reserves.

The effects of spittlebug feeding on susceptible plants (*B. decumbens*) compared to feeding on resistant plants (*B. brizantha*) is shown in Table 3. Reductions in plant weight due to nymphal feeding

TABLE 1 Mean weight differences (mg) and percent reduction between control plants and infested plants during the time insects are feeding, at the time insects are removed, and after the insects have been of the plants for a certain number of days 1986¹

Test Test number and treatments	Insect on plants 10 days						Time of insect removal from plants						Ten days after insect removal						Twenty days after insect removal						Average % reduction per treatment	
	Foliage			Roots			Foliage			Roots			Foliage			Roots			Foliage			Roots				
	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.	$\bar{X}$	S.E.	% Red.		
1 ² Small nymphs Control	-	-	-	-	-	-	136 a	8.53	20	27 a	1.46	21	-	-	-	-	-	-	-	-	-	-	-	-	-	
2 ³ Large nymphs Control	167 a	14.46	13	41 a	1.93	21	307 a	18.10	18	103 a	6.55	20	550 a	43.59	28	172 a	19.00	51	422 a	39.18	58	93 a	11.09	75	36	
3 ⁴ Large nymphs and adults Control	193 a	12.93	52 b	52 b	3.15	-	374 b	25.40	-	128 a	10.84	-	739 b	40.13	-	350 b	24.61	-	758 b	34.04	24	365 c	22.59	365 c	22.59	
4 ⁵ Adults (A) Control	-	-	-	-	-	-	241 a	12.81	20	107 a	8.73	35	402 a	28.84	30	108 a	18.17	40	422 a	39.18	58	93 a	11.09	75	36	
Adults (B) Control	-	-	-	-	-	-	298 b	19.26	3	107 a	9.31	35	457 a	44.69	21	123 a	13.25	32	758 b	34.04	24	365 c	22.59	365 c	22.59	
Adults (B) Control	-	-	-	-	-	-	301 b	17.81	-	164 b	20.87	-	578 b	25.61	-	180 b	11.33	-	953 c	40.98	-	-	-	-	-	
Adults (A) Control	-	-	-	-	-	-	963 a	85.70	2	284 a	31.32	8	1044 a	69.56	6	520 a	41.37	8	-	-	-	-	-	-	-	
Adults (B) Control	-	-	-	-	-	-	982 a	53.29	-	310 a	13.91	-	1107 a	98.73	-	552 a	18.71	-	-	-	-	-	-	-	-	
Adults (B) Control	-	-	-	-	-	-	921 a	80.80	18	268 a	30.58	31	1004 a	75.00	28	621 a	51.94	9	-	-	-	-	-	-	-	
Adults (B) Control	-	-	-	-	-	-	1126 a	95.09	-	391 b	22.94	-	1387 b	81.08	-	686 a	35.71	-	-	-	-	-	-	-	-	

1¹ Infestation rate for both nymphs and adults = 2 insects/plant.Plants = *Brachiaria decumbens*; S.E = Standard error, Means within a column followed by the same letter are not significantly different ($P < 0.05$; Duncan's multiple range test).2² Nymphs on plants 16 days; age of plants 30 days.3³ Nymphs on plants 20 days; age of plants 36 days.4⁴ Nymphs on plants 7 days; adults on 3 days; age of plants 43 days.5⁵ Adults (A) on plants 4 days, Adults (B) on plants 7 days; age of plants 66 days.

TABLE 3. Mean weight differences (mg) and percent reduction between control plants and infested plants of *B. decumbens* and *B. brizantha* at the time the insect are removed from the plants and for certain time periods following insect removal, 1961¹

Test number and treatments	Time of insect removal from plants						Seven days after insect removal						Eleven days after insect removal						Twenty one days after insect removal						Twenty eight days after insect removal						Ar. % reduction per treatment	
	Foliage			Roots			Foliage			Roots			Foliage			Roots			Foliage			Roots			Foliage			Roots				
	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*	X	SE	% R*		
7. <i>Brachiaria decumbens</i>²																																
Control	621 a	62.38		216 a	14.79		1387 a	75.24		368 a	18.53		1709 a	131.84		357 a	18.76		2971 a	121.00		958 a	67.56		2971 a	121.00		958 a	67.56		78.8	26.8
2 adults/plant	552 a	33.94	11	103 b	15.45	52	864 b	108.72	38	282 a	27.81	23	1092 b	125.00	36	368 a	56.54	0	2078 b	232.83	30	648 b	29.05	32								
8. <i>Brachiaria brizantha</i>³																																
Control	928 a	41.83		509 a	46.93		1115 a	48.26		667 a	59.16		1156 a	36.42		532 a	21.92		1403 a	42.62		1125 a	33.72									
2 adults/plant	891 a	31.75	4	325 b	27.69	38	978 b	30.91	12	804 a	42.70	9	1052 a	32.18	9	609 a	39.53	0	1477 a	31.63	0	1658 a	85.00	6								
Control	872 a	36.84		374 a	28.01								1063 a	35.19					1215 a	33.86		488 a	17.69									
2 nymphs/plant	806 a	39.00	8	290 a	29.64	12							1102 a	55.01	0				1249 a	65.81	0	572 a	48.24	0								
9. <i>Brachiaria brizantha</i>³																																
Control	387 a	9.82		243 a	27.90		646 a	25.49		392 a	30.57		833 a	19.59		824 a	61.79		1119 a	37.66		398 a	26.91									
3 adults/plant	290 b	11.21	21	119 b	10.79	51	522 b	33.31	19	96 b	10.77	78	880 a	75.28	18	108 b	58.03	83	900 b	42.12	20	537 b	39.48	0	1310 a	42.63		485 a	36.40			
Control	705 a	60.25											1183 a	90.42																		
2 nymphs/plant	548 b	26.88	22										1012 a	64.82	15																	

¹ S.E. = standard error. Means within a column followed by the same letter are not significantly different ($P < 0.05$; Duncan's multiple range test).

² Nymphs on plants 10 days, and adults 3 days; age of plant 70 days.

³ Nymphs on plants 10 days, and adults 4 days; age of plants 50 days.

* R = reduction.

TABLE 4. Summary of statistical comparisons between control and infested treatments in tests shown in Tables 1, 2 and 3.

Insect group	Insect density	Infestation time	Number of comparison	Number not significant	Number significant	Percent reductions from tests that were significant	Average % reduction	Combined averages according to nymphs adults or combination
<i>(B. decumbens)</i>								
Nymphs (instars 1, 2 + 3)	2/plant	18 days	Foliage 1	0	1	20	20	Foliage roots 21 36
Nymphs (instars 4 + 6)	2/plant	20 days	Roots 1	0	1	21	21	
Adults	2/plant	3-7 days	Foliage 2	0	2	18 28	22	27 49
			Roots 2	1	1	81	81	
Adults	2/plant	3-7 days	Foliage 16	10	6	21 24 28 38 36 30	30	36 50
			Roots 16	6	10	35 32 24 21 52 32	37	
Adults	4/plant	3-5 days	Foliage 8	3	5	51 38 43 33	37	36 50
			Roots 8	2	6	33 27 24 24 10	24	
Adults	8/plant	3-5 days	Foliage 3	1	2	42 65 60 56 68 66	60	36 50
			Roots 3	1	2	28 16	21	
Adults	16/plant	3-5 days	Foliage 3	1	2	30 36	33	36 50
			Roots 3	1	2	41 20	31	
Nymphs + adults	2 nymphs/plant + 2 adults/plant	Nymphs - 7 days Adults - 3 days	Foliage 3	0	3	77 80	79	36 50
			Roots 3	0	3	20 30 58	36	
<i>(B. brizantha)</i>								
Nymphs (instars 3, 4 + 5)	2/plant	10 days	Foliage 5	4	1	22	22	19 62
			Roots 2	2	0	—	—	
Adults	2/plant	3 days	Foliage 4	3	1	12	12	19 62
			Roots 4	3	1	36	36	
Adults	3/plant	4 days	Foliage 5	1	4	21 19 20 24	21	19 62
			Roots 5	2	3	61 76 83	70	

were much lower on *B. brizantha* plants than on *B. decumbens* plants. Out of seven comparisons (Table 4) of differences due to nymphal feeding on *B. brizantha*, only one was significantly ($P < 0.05$) different. One half of the comparison of plant weight (foliage and roots) due to adult feeding on *B. brizantha* were not significant ($P > 0.05$) (Table 4). There also was a tendency for infested plants of *B. brizantha* to equal or surpass the weight of the control plants after the insects were removed. This did not usually happen with the infested plants of *B. decumbens*.

From the available evidence it appears that both foliage and root production of *B. decumbens* can be drastically reduced by spittlebug feeding. The degree of reduction while dependent upon several factors is certainly effected by insect density, insect stage, and the duration of insect feeding. In central Brazil at the start of the rainy season, nymphal feeding occurs for about a two-month period prior to the appearance of large populations of adults. This is followed by 6-7 months when both nymphs and adults are feeding on available forage. During heavy infestations it is likely that all plants are fed upon by both nymphs and adults over this extended period of time. Spittlebug-free pasture are rare in central Brazil, thus production seldom reaches its potential. Since spittlebug feeding does reduce available forage and root development then prolonged periods of feeding can be expected to be detrimental to future productivity and stand persistence.

CONCLUSIONS

1. The average weight reduction of the foliage and roots of *B. decumbens* due to spittlebug feeding was as follows: nymphs (foliage 21%, roots 36%), adults (foliage 27%, roots 48%) and nymphs plus adults (foliage 36%, roots 50%).

2. Forage reductions due to adult feeding were evident as early as three days from the time the insects began to feed.

3. Reductions in root weights due to insect feeding was about $1\frac{1}{2}$ time greater than reductions to the above ground plant portion.

4. In general, damage was in direct proportion to insect density. Foliage reduction ranged from 11% at two adults/plant to 27% at 16 adults/plant. Root reduction averaged 35% at two adults/plant.

5. Differences in plant weights between control plants and infested plants due to spittlebug feeding were less on *B. brizantha* plants than on *B. decumbens* plants. More comparisons in plant weights were significantly ($P < 0.05$) different in the *B. decumbens* treatments than in the *B. brizantha* treatments. Thus *B. brizantha* was less affected by spittlebug feeding. *Brachiaria brizantha* recovered more rapidly from spittlebug feeding than did *B. decumbens*.

6. Significantly ($P < 0.05$) more new shoots were produced on *B. decumbens* plants that had been fed on by high densities of adults.

ACKNOWLEDGEMENTS

This work was conducted while on assignment with Inter-American Institute for Cooperation on Agriculture Organization of American States, San José, Costa Rica and Empresa Brasileira de Pesquisa Agropecuária on CNPQC, project number 800.84.078/7. The author thanks Drs. Shashank S. Nilakhe and Marcio Antonio Naves for technical support and Irineu Cavicchione, Lélia Inês Zampieri Vera, and Marlene Conceição Monteiro for laboratory and field assistance.

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Mechanical limitations on feeding by meadow spittlebugs *Philaenus spumarius* (Homoptera: Cercopidae) on wild and cultivated host plants

GEORGE D. HOFFMAN* and PETER B. McEVOY Department of Entomology,
Oregon State University

ABSTRACT. 1. Field observations on the distribution of *Philaenus spumarius* (L.) on pearly everlasting (*Anaphalis margaritacea*) and alfalfa (*Medicago sativa*) showed that the range of feeding sites exploited increased with instar. Development of trichomes, depth of xylem elements, and tissue hardness were measured as possible factors determining the suitability of sites on food plants.

2. Spittlebugs caged outside their normal feeding sites experienced difficulty feeding. Experimental removal of trichomes showed that trichomes prevented younger instars from feeding on the stem. The depth of the xylem elements and tissue hardness were not significant barriers to feeding near the stem apex.

3. By caging fourth and fifth instar nymphs at increasing distances below the terminal bud on *A. margaritacea* stems, we showed feeding ability declined with distance below the apex, and feeding was more restricted in fourth compared to fifth instars. A similar decline was demonstrated in experiments with fifth instars on *M. sativa*.

4. On *A. margaritacea*, this restriction was associated with increasing tissue hardness of the stem with distance from the apex and the presence of trichomes in regions with hard tissues. On *M. sativa* the associated barriers were a combination of tissue hardness and reduction in the availability of xylem vessels in the penetrable region of the stem. Although the tissues impeding stylet penetration differed in the two hosts, the critical factor in both species was the increase in the amount of lignification of those tissues at increasing distances from the terminal bud.

Key words. Spittlebugs, Cercopidae, *Philaenus*, plant anatomy, insects and host plants, trichomes, tissue hardness, mechanical defences.

*Present address: Department of Entomology, University of Wisconsin.

Correspondence: Dr Peter B. McEvoy, Department of Entomology, Oregon State University, Corvallis, OR 97331, U.S.A.

Introduction

Mechanical defences of plants have long been of practical importance in breeding plants resistant to insects (Painter, 1951; Norris & Kogan, 1980), but they have been neglected as determinants of feeding specialization for insects colonizing natural plant communities. This study compared mechanical limitations on feeding by the meadow spittlebug *Philaenus spumarius* (L.) on wild and cultivated host plants.

The distribution of *P. spumarius* on individual host plants has been correlated with external physical gradients (Whittaker, 1970), availability of water (Weaver & King, 1954) or amino acids (Horsfield, 1977) within the plant, and mechanical barriers (McEvoy, 1985). Correlations lead to predictive statements about the distribution of nymphs on host plants, but they do not expose the factors which set limits to the distribution. To reveal the true extent and the proximate cause of restricted distribution we transplanted nymphs outside their normal feeding sites and observed their behaviour at these alien sites. We investigated plant anatomical barriers known to interfere with other stylet-feeding insects: trichomes (Painter, 1951; Levin, 1973; Webster, 1975); tissue hardness (Staniland, 1924; Entwistle & Longworth, 1963; Knight & Alston, 1974; Horsfield, 1977); and depth of the feeding sites (Houston *et al.*, 1947; Day *et al.*, 1952; Chatters & Schlehuber, 1951; Gibson, 1972; Quiros *et al.*, 1977). We assessed the role of trichomes by experimental removal and the effect of barriers inside the stem by study of stylet behaviour in relation to stem anatomy as revealed by histological sections.

Methods and Materials

Species studied

P. spumarius is a univoltine species; overwintering eggs hatch in early spring and nymphs develop through five instars, moulting to the adult in early summer. The insect feeds by piercing intercellularly with its stylets to the xylem vessels and ingesting the sap (Wiegert, 1964; Horsfield, 1978). The nymphs produce 'spittle', a foamy liquid formed by the introduction of air bubbles into the copious watery excrement (Weaver & King, 1954). A spittle-

mass is evidence of feeding by a nymph at that location on the plant.

We studied the distribution of nymphs on a native perennial herb, pearly everlasting *Anaphalis margaritacea* D.C. (Asteraceae), growing at Marys Peak (elevation 700 m), Benton Co., Oregon; and on alfalfa *Medicago sativa* L. var. Du Puits (Fabaceae) growing in a 3-year-old stand in the Willamette Valley, Benton Co., Oregon. Plants and insects were collected from these sites for laboratory caging experiments.

Field distribution and its anatomical correlates

The feeding sites of the five instars were recorded approximately weekly on *A. margaritacea* during 1979 and 1980. All plants within a 1 m radius of randomly selected points were examined for spittlemasses. Nymphs from each mass were collected and the instar determined according to criteria given by Weaver & King (1954). We measured the height of each plant, the distance of each spittlemass below the terminal bud, and noted whether the spittlemass was on the stem or leaf. The distance below the terminal bud (DBTB) was chosen as a descriptive variable because tissue hardness increases as stem tissues mature. Maturation follows stem elongation and occurs at a characteristic distance below the terminal bud (Esau, 1977). Representative segments of host plants were preserved in formalin-acetic acid-alcohol (FAA) for later analysis.

The distribution of the fifth instar on *M. sativa* was recorded in spring 1980. Data collection was identical to that on *A. margaritacea* except that spittlemasses on the main stem were distinguished from those on the side branches.

The preserved plant tissue was examined microscopically to identify differences in the external and internal stem anatomy between the used and unused portion of the plant. Segments were dehydrated in a series of tertiary-butyl-alcohol solutions and embedded in paraffin. The 10 μ m serial sections were stained with safranin and fast green (Johansen, 1940).

Manipulative experiments

To test the suitability of feeding sites, nymphs were confined individually in cages with mesh sides, plastic bottoms and tops, and

a hole lined with mesh to accommodate the stem while avoiding compression of the trichomes. Cages did not interfere with feeding: fifteen first instar nymphs caged on leaves of *A. margaritacea* quickly formed spittlemasses. Experiment 1 tested the ability of instars 1–5 to feed on the stem at the apex of *A. margaritacea*. Cages in the first experiment were half cylinders, 2 cm in diameter and 0.3–0.6 cm high. Experiment 2 tested the ability of the older nymphs to feed at increasing DBTBs along the stems of *A. margaritacea* and *M. sativa*. Cages in the second experiment were full cylinders, 2 cm in diameter and 0.5–0.8 cm high. Plants bearing caged nymphs were placed at 20–25°C and 30–50% r.h., and left until nymphs had formed a spittlemass or dehydrated and died. The feeding nymphs were frozen on the stem with cold CO₂ so that the approximate location of the stylets could be marked. All stem segments were preserved in FAA for later sectioning.

Feeding ability was compared on *A. margaritacea* stems with trichomes intact and on stems with trichomes removed. We shaved trichomes from the entire caged area in experiment 1, and a quarter of the caged area in experiment 2. The height of the trichome layer, its density/mm², and the vertical density of trichomes were measured using the methods of Hoffman & McEvoy (1985).

Stylet sheaths (stained with safranin) were studied in the histological sections (10 µm) to discover anatomical features encountered during probing. The stylet sheath is formed as the stylets are inserted and remains in the tissue after stylets are withdrawn, forming a permanent record of stylet behaviour during the feeding process (Pollard, 1968).

We evaluated the depth of the feeding sites by comparing the maximum penetrable distance (MPD) for each instar to the depth of the xylem vessels at the caging site. To obtain estimates of MPD, we multiplied the 'usable fraction' of stylet length for first instars (the ratio of the longest stylet sheaths (four of sixteen sheaths) to the mean external stylet length for twenty-five nymphs) times the stylet length for each instar (Hoffman, 1983). The minimum and median depths of xylem vessels were estimated for a randomly chosen vascular bundle in each quarter of a randomly chosen section.

Data analysis

The response variable, presence or absence of feeding, is binary and thus likely described by a logistic function (Neter & Wasserman, 1974). We used stepwise logistic regression to determine the significance of variables entered in the model. The significance of each step selection was evaluated using the log of the ratio of current versus previous maximum likelihood function values. Under the null hypothesis of no significant improvement, this ratio is distributed as chi-square with 1 d.f. (Dixon, 1981). In cases where the predicted probability of feeding at the control site (5 or 10 cm BTB) was less than 0.99, a dummy variable (CONTROL) was used to designate this DBTB as a control. This moved the fitted regression curve to within a 0.99 probability at the control site and had a negligible effect upon the significance of adding a particular variable to the model.

Results

Field distribution and its anatomical correlates

The range of feeding sites increased with instar (Fig. 1a). On *A. margaritacea*, the young instars (1–3) fed almost exclusively on the leaves of the upper stem. The percentage feeding on the stem increased as the nymphs matured to later instars. Nymphs fed only at the apex of the host; the proportion of stem length utilized increased slightly with each instar. The range of stem feeding sites of the fifth instar extended to 8 cm below the terminal bud (Fig. 1a). On *M. sativa*, fifth instar *P. spumarius* nymphs also fed on a small proportion of the stem (Fig. 1b). Its feeding range extended to 28 cm BTB on the main stem and 25 cm BTB on the side branches.

Variation in the incidence of feeding was associated with variation in the development of several anatomical structures (Hoffman, 1983). In *A. margaritacea* these were lanate trichomes, tissue hardness, and depth of the xylem vessels; in *M. sativa* they were tissue hardness, depth of the xylem vessels and availability (number and area) of xylem vessels. Each of these correlates was evaluated in manipulative experiments.

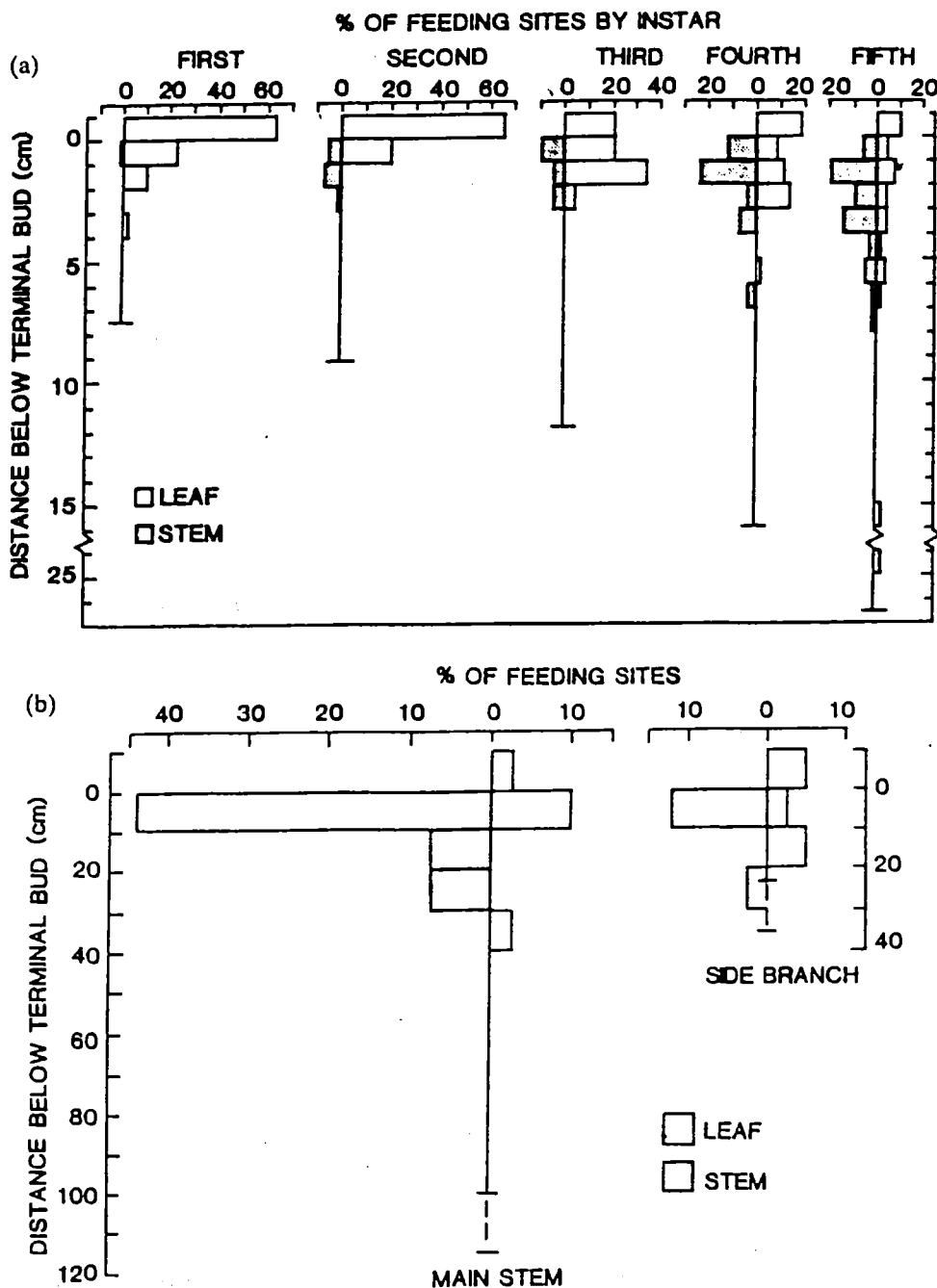


FIG. 1. Distribution of *P. spumarius* nymphs on host plants: (a) instars 1-5 on *A. margaritacea*, *N* for instars 1-5=49, 58, 23, 70, 69; (b) fifth instars on *M. sativa*, *N*=41.

Manipulative experiments

Effects of caging outside normal feeding range. Nymphs caged outside their normal feeding sites on *A. margaritacea* had difficulty feeding. In experiment 1 the percentage of caged nymphs able to feed on the stem increased significantly with instar (Fig. 2, Appendix). Few nymphs in instar 1-3 were able to feed when caged on stems bearing trichomes. The fourth instar nymphs were able to feed on the stem, but were slow to initiate spittlemasses.

Eight of the fifteen nymphs had not formed a spittlemass after 45 min, and two took as long as 4.5 h. The fifth instar nymphs fed readily on stems bearing trichomes; all formed masses within 45 min. In experiment 2 the percentage of fourth and fifth instar nymphs able to feed decreased with an increase in DBTB on *A. margaritacea* (Fig. 3a, b - trichomes present, Appendix). The relationship between the feeding ability of the fifth instar and DBTB did not differ in 1980 and 1982 (logistic regression, $\chi^2=0.03$, 1 df, $P=0.868$), so these data were

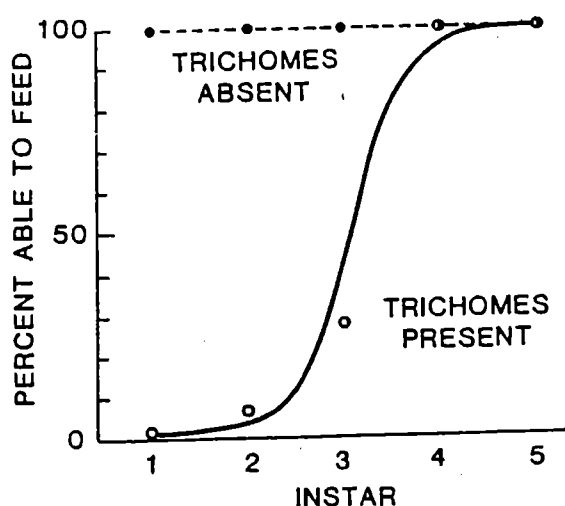


FIG. 2. Percentage of first to fifth instar nymphs able to feed when caged on the stem of *A. margaritacea* with trichomes present and absent. Regression curves fitted by hand through predicted values. Regression coefficients and significance levels listed in Appendix. Goodness-of-fit of the model, $\chi^2 = 3.527$, 8 df, $P = 0.897$.

pooled. The time required by fifth instar nymphs to initiate a spittlemass increased with DBTB, providing further evidence of increase in feeding difficulty with increase in DBTB (Fig. 4).

The ability of the fifth instar to feed below its normal feeding range declined slightly but significantly on *M. sativa* with an increase in DBTB (Fig. 3c, Appendix).

Effects of trichomes on feeding. Trichomes were a barrier to feeding on *A. margaritacea*. In experiment 1, 100% of the nymphs in instars 1–5 were able to feed when caged at the apex of stems from which trichomes had been removed (Fig. 2). Significant improvement in the logistic regression model was obtained by addition of the variable representing presence or absence of trichomes (Appendix). Histological sections of eight shaven stem segments upon which first instar nymphs had fed confirmed that stylet sheaths reached xylem elements.

In experiment 2, trichomes reduced the percentage able to feed on *A. margaritacea* for the fourth (Fig. 3a, Appendix) and fifth (Fig. 3b, Appendix) instars. We estimated the resistance added by the trichomes as the difference between the regression curves for trichomes absent v. trichomes present. Three conclusions may be drawn from these estimates. First, the resistance added by trichomes was greater for fourth compared to fifth instars (Fig. 3a, b).

Second, the level of trichome resistance to fourth instars was similar over all DBTB below the normal feeding range, whereas the level of trichome resistance to fifth instars first increased to a maximum then declined with increasing DBTB (Fig. 3b); however, the interaction term in the model (DBTB $\times$ TRICHOME) was only marginally significant ($P = 0.07$, Appendix). Third, among nymphs successfully feeding on stems with trichomes partially removed, a high and constant percentage (73%) of fourth instar nymphs fed at the shaven spot; whereas in fifth instar nymphs, the association with the shaven spot was variable, increasing with increasing trichome resistance (Fig. 5).

Variation in trichome resistance with DBTB was not accompanied by significant variation in horizontal density, vertical density, or height of trichomes (Table 1). We concluded that variation in the effect of trichome removal probably arises from an interaction between trichomes and some other factor (e.g. tissue hardness), rather than variation in trichomes *per se*.

Other anatomical barriers to feeding

Since nymphs fed readily on the apex of *A. margaritacea* stems from which trichomes had been removed, there were apparently no barriers restricting access to the xylem inside the apical portion of the stem. The depth of the xylem vessels did not exceed the reach of the stylets: the maximum penetrable distance ($\bar{x} \pm \text{SD}$) of the first instar (Table 2) exceeded the median depth of xylem vessels at the apex (Table 1) ($t = 98.57$, 38 df, $P \leq 0.001$). Tissue hardness did not appear to be a barrier: all nymphs on the shaven stem were able to feed and sectioned stems on which the first instars were caged showed no tissues interfering with stylet penetration. We concluded trichomes were the sole factor preventing nymphs from feeding on the apex of *A. margaritacea* stems.

Internal barriers restricted nymphs from feeding lower on *A. margaritacea* stems, as evidenced by a decline in percentage feeding with DBTB for fourth and fifth instars on stems lacking trichomes (Fig. 3a, b; Appendix). The percentage feeding decreased faster with increasing DBTB for fourth compared to fifth instars (Logistical Regression, $\chi^2 = 34.972$, 1 df, $P < 0.0005$), suggesting the ability to overcome barriers inside the stem increases with spittlebug size.

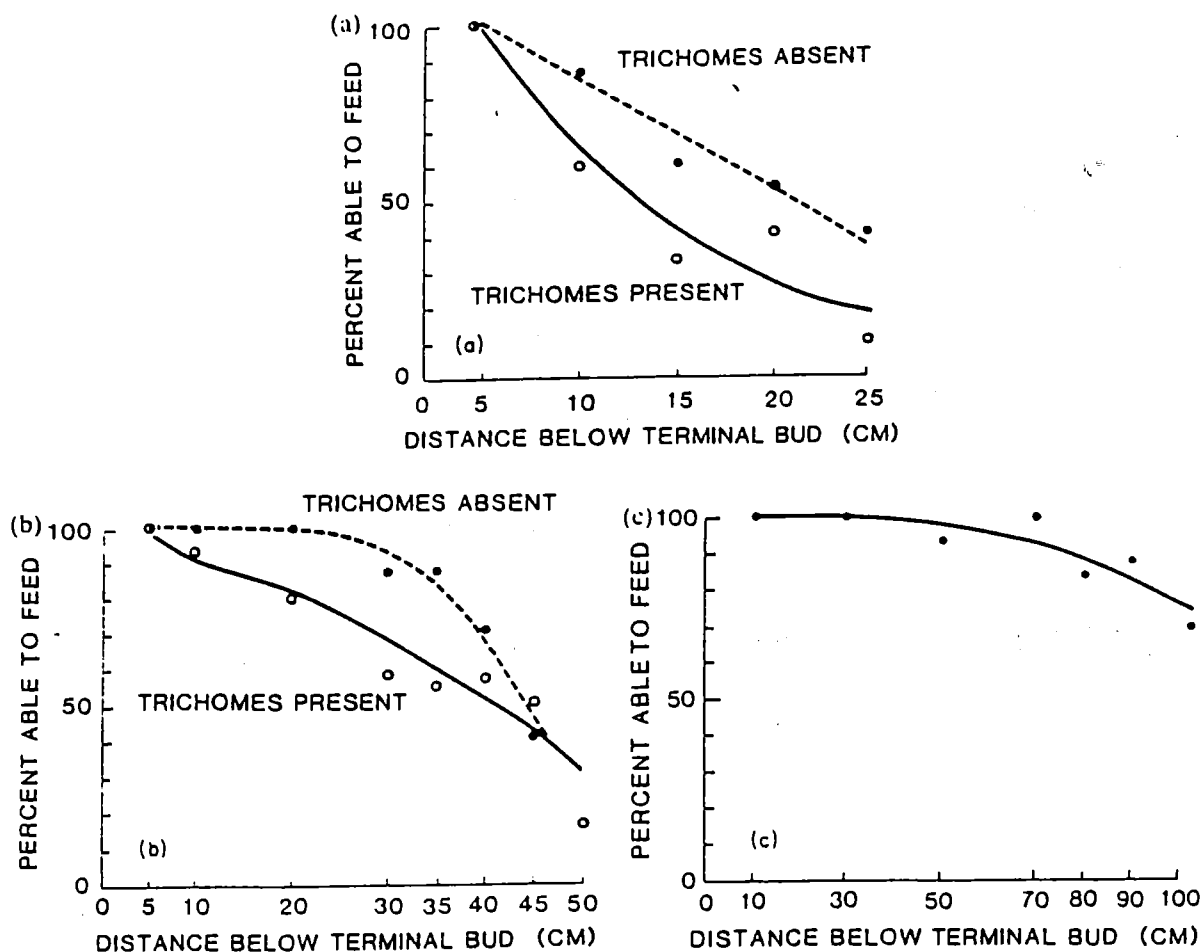


FIG. 3. Percentage of nymphs able to feed when caged at increasing distances below the terminal bud. Regression curves fitted by hand through predicted values. Regression coefficients and significance levels listed in Appendix. (a) Fourth instar on *A. margaritacea*. N at increasing DBTB=15, 15, 15, 15, 10. Goodness-of-fit for model with variables DBTB and TRICHOME: $\chi^2=2.838$, 7 df, $P=0.900$. (b) Fifth instar on *A. margaritacea*. N at increasing DBTB: for stems with trichomes present=31, 31, 31, 31, 26, 18, 12; for stems with trichomes absent=15, 15, 15, 15, 10, 5. Goodness-of-fit for model with variables DBTB, TRICHOME, DBTB $\times$ TRICHOME: $\chi^2=5.859$, 11 df, $P=0.883$; with variables DBTB, TRICHOME: $\chi^2=9.15$, 12 df, $P=0.690$. (c) Fifth instar on *M. sativa*. N at increasing DBTB=15, 15, 15, 15, 13, 8, 7. Goodness-of-fit of the model with variable DBTB: $\chi^2=3.601$, 5 df, $P=0.608$.

(a) Tissue hardness. We inferred that tissue hardness impeded stylet penetration on *A. margaritacea* in cases where stylet sheaths terminated at lignified tissues (Table 3), assuming that stylets did not probe beyond the point of termination of the sheath (Pollard, 1968). Within the normal feeding range (0–8 mm DBTB), stem tissues were elongating and neither the immature fibres of the bundle cap nor the interfascicular parenchyma cells deterred stylet penetration (Fig. 6a). At 10 cm DBTB the first traces of lignin appeared in the bundle cap and it started to form a barrier to penetration (Fig. 6b). With the pathway to the xylem through the vascular cap becoming more difficult to penetrate at greater DBTB, the nymphs increasingly reached the xylem by

penetrating the interfascicular region (Fig. 6c). If the number of cell layers forming the cap was small, the nymphs were able to penetrate the lignified bundle caps: the stylets often travelled intercellularly rather than intracellularly. At 15–20 cm DBTB, the interfascicular region became lignified and restricted the alternate pathway to the xylem (Fig. 6d). The larger fifth instar nymphs were able to penetrate these hard tissues with greater frequency than the fourth instar nymphs. If the stylets did penetrate to the xylem tissue at the lower caging sites, the lignified xylem fibres were an additional barrier to reaching the xylem vessel.

The stem tissues impeding stylet penetration in alfalfa differed from those in *A. margaritacea* and offered less resistance (Table 4). Stylet

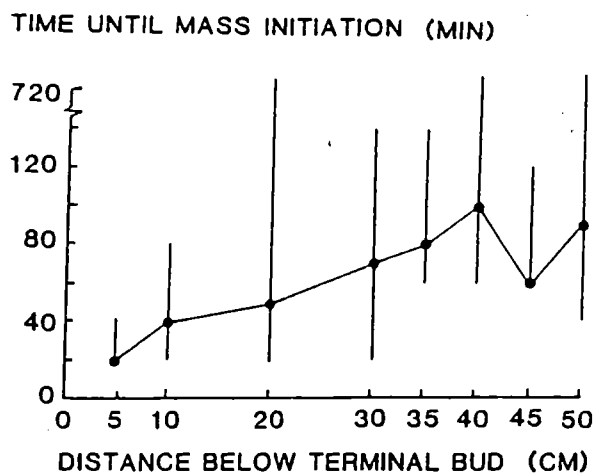


FIG. 4. Time until spittlemass initiation (median, range) for fifth instar nymphs forming masses at increasing distances below the terminal bud on *A. margariacea*. *N* at increasing DBTB=13, 12, 10, 6, 8, 8, 5, 2. There is a significant positive correlation between the two variables (Kendall's rank correlation, $r=0.7143$, $P=0.0071$).

sheaths penetrated the bundle cap, composed of non-lignified collenchyma cells, in fifteen of nineteen cases at 30–100 cm BTB (Fig. 6e). Stylet sheaths also penetrated the non-lignified interfascicular region between the bundle caps. The major obstacle to penetration of xylem vessels was increasing lignification in xylem fibres with increase in DBTB. The fifth instar could penetrate a maximum of four heavily lignified fibre cells, and sometimes terminated penetration upon encountering the first lignified fibre of the peripheral xylem. The combination of tissue hardness and the low proportion of peripheral xylem vessels in the lower stem reduced the availability of xylem vessels (Fig. 6f). The decrease in percentage feeding at 50–90 cm BTB was associated with an increase in tissue hardness: the availability of

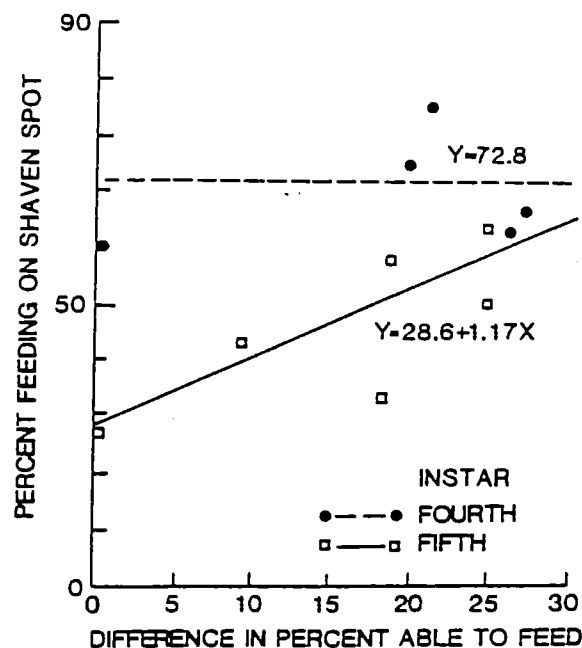


FIG. 5. Percentage of *P. spumarius* nymphs feeding on shaven spot on *A. margariacea* versus trichome resistance (measured as the difference in percentage able to feed on stems with trichomes present or partially absent). Significance of regressions: fourth instar, Regression ANOVA, $F=1.16$, 1, 3 df, $P=0.3601$, ns; fifth instar, Regression ANOVA, $F=10.44$, 1, 4 df, $P=0.032$. Point at 45 cm DBTB excluded because of small sample size.

xylem vessels was approximately constant in this region (Table 5).

(b) Xylem depth. The depth of the xylem elements in *A. margariacea* (Table 1) was well within the maximum penetrable distance of the stylets of fourth and fifth instars (Table 2). At 40 cm BTB the average depth of the median xylem vessel was significantly less than the MPD of the fourth ($t=69.83$, 28 df, $P\leq 0.001$) and fifth ($t=119.19$, 28 df, $P\leq 0.001$) instars. The longest stylet sheaths found in the sec-

TABLE 1. Depth of xylem elements and characteristics of the trichome layer ($\bar{x} \pm \text{SE}$) for *A. margariacea*. Mean within a column followed by the same letter are not significantly different ($P>0.05$) according to ANOVA and Tukey's HSD multiple comparisons. If variances were significantly heterogeneous (Bartlett's test), tests were made on log transformed data. *N*=20 throughout, four measurements (one in each quarter of the stem circumference) for one section from each of five plants.

Distance below terminal bud (cm)	Depth of xylem element (mm)		Characteristics of the trichome layer		
	Minimum	Median	Density/mm ²	Vertical density*	Height (mm)
5	0.191 $\pm$ 0.014 ^a	0.227 $\pm$ 0.013 ^a	261 $\pm$ 48 ^a	34 $\pm$ 7 ^a	0.441 $\pm$ 0.055 ^a
10	0.202 $\pm$ 0.009 ^a	0.267 $\pm$ 0.012 ^{ab}	204 $\pm$ 26 ^a	25 $\pm$ 5 ^a	0.321 $\pm$ 0.033 ^a
20	0.204 $\pm$ 0.010 ^a	0.272 $\pm$ 0.019 ^{ab}	194 $\pm$ 15 ^a	25 $\pm$ 4 ^a	0.328 $\pm$ 0.044 ^a
30	0.210 $\pm$ 0.006 ^a	0.293 $\pm$ 0.019 ^{ab}	187 $\pm$ 40 ^a	21 $\pm$ 2 ^a	0.326 $\pm$ 0.067 ^a
40	0.222 $\pm$ 0.005 ^a	0.338 $\pm$ 0.022 ^b	179 $\pm$ 10 ^a	20 $\pm$ 2 ^a	0.372 $\pm$ 0.033 ^a

* Vertical density is total number of intercepts for five perpendicular lines.

TABLE 2. The maximum penetrable distance ($\bar{x} \pm \text{SE}$, $N=25$) of the five nymphal instars of *P.spumarius*.

Instar	Maximum penetrable distance (mm)
1	0.265 $\pm$ 0.003
2	0.359 $\pm$ 0.004
3	0.466 $\pm$ 0.004
4	0.658 $\pm$ 0.005
5	0.870 $\pm$ 0.008

tioned material were 0.36 and 0.41 mm for the fourth and fifth instars respectively; these sheaths passed through the interfascicular region, missed the xylem vessel, and terminated at the pith. While these were shorter than the MPD, they were longer than the depth of the median xylem vessel at the base of the stems (Table 1).

The depth of the median xylem vessel in *M.sativa* at the lowest caging site (90 cm) (Table 5) was less than the MPD for the fifth instar (Table 2) ($t=29.74$, 28 df, $P \leq 0.001$). The number of xylem vessels and the percentage of the xylem circumference containing xylem vessels decreased by 50% with the increase in DBTB (Table 5), suggesting that

decreased availability of xylem vessels in the lower stem may contribute to the decrease in percentage feeding.

Discussion

All nymphs fed successfully when caged within their normal feeding range but experienced difficulty when caged outside this range. Nymphs that managed to feed outside their normal range required a longer time to initiate a spittlemass. In the field, delay in forming a mass probably exposes the nymphs to greater risks from thermal stress, desiccation (Wiegert, 1964), and natural enemies (Whittaker, 1970).

Anatomical barriers contribute to the difficulty spittlebugs experienced in attempts to feed outside the normal range, but the specific barriers varied among spittlebug instars and between host species. On *A.margaritacea*, experimental removal of trichomes showed that trichomes prevented younger instars from feeding on the stem. Restricted feeding by older instars on this host is associated with increasing tissue hardness of the stem with

TABLE 3. Number of stylet sheaths in a given location for fourth and fifth instars of *P.spumarius* on *A.margaritacea*. Shown are the number of sheaths which penetrate (=pen.) or terminate at or in (=term.) a given tissue. Number of plants examined: ten for fourth instar and five for fifth instar.

DBTB	Stylet sheath location							
	To vascular caps				Between vascular caps			
	Instar 4		Instar 5		Instar 4		Instar 5	
	Pen.	Term.	Pen.	Term.	Pen.	Term.	Pen.	Term.
5	7	0	2	0	4	0	2	0
10	4*	4	2	1	1	0	4	0
15	2*	8			3	3		
20	1*	8	2*	3	5	13	4	1
25	1*	4			1	2		
30-35			1*	8			2	5
40-45			0	15			5	2
50			0	4			0	3

*Stylet went through a thin cap on edge of the cap.

FIG. 6. Stem tissues of *A.margaritacea* in relation to stylet penetration by the fourth instar: (A) stylet sheath through the unligified primary cell walls of the bundle cap at 5 cm BTB; (B) stylet sheath terminating in the bundle cap at 10 cm BTB; (C) maxillary stylet penetrating interfascicular region at 15 cm BTB and entering xylem vessel; (D) stylet sheath terminating in interfascicular parenchyma which has developed lignified secondary cell walls. Stem tissues in *M.sativa* in relation to stylet penetration by the fifth instar: (E) stylet sheath through bundle cap at 100 cm BTB; (F) stylet sheath through bundle cap and terminating in lignified fibre cells short of xylem vessels. at 50 cm BTB. S=stylet sheath; X=xylem vessel.

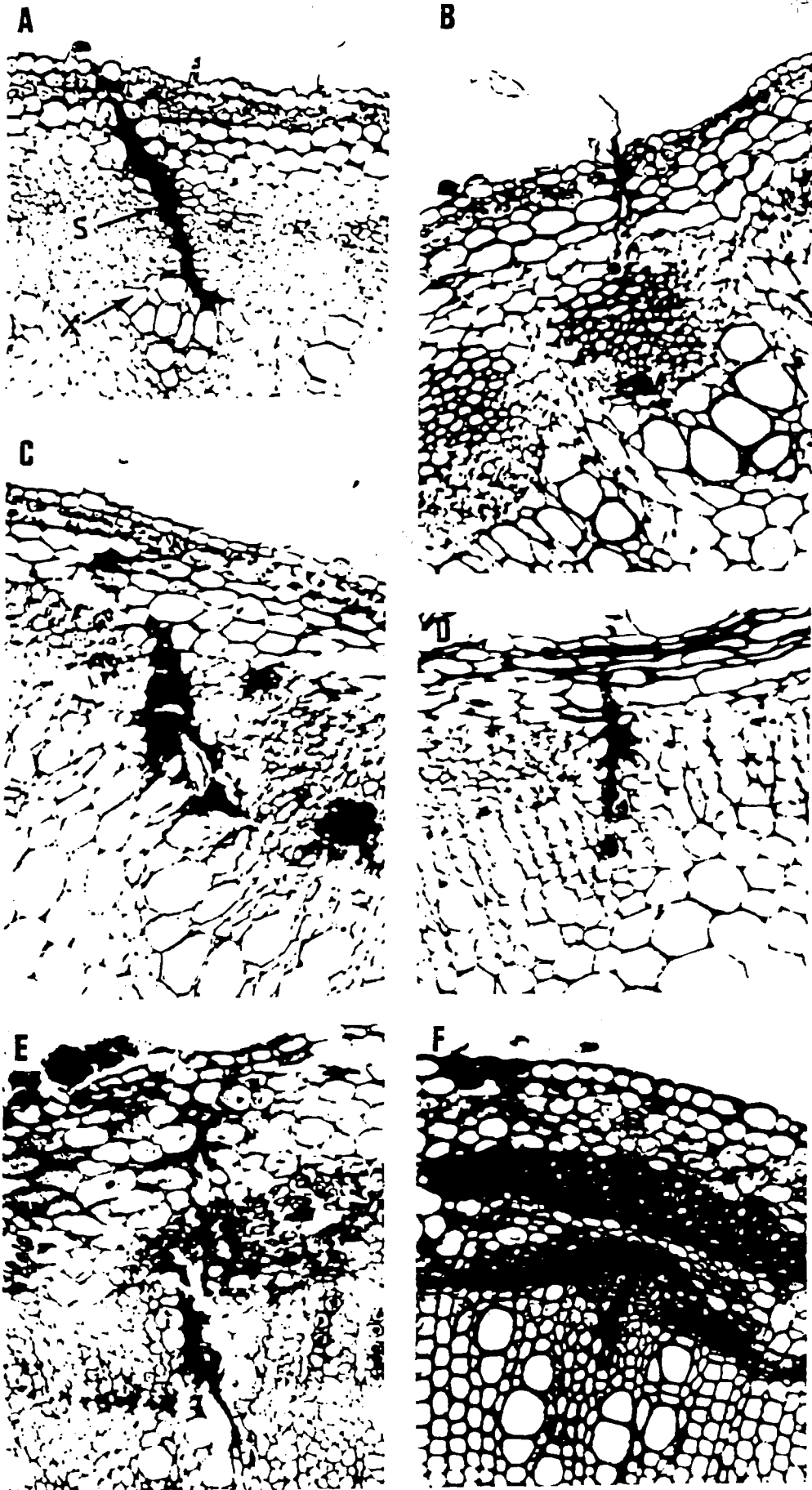


TABLE 4. Number of stylet sheaths in a given location for fifth instar *P.spumarius* on *M.sativa*; five plants examined.

DBTB (cm)	To vascular caps			Between vascular caps		
	Penetrate		Terminate	Penetrate		Terminate
	To xylem vessel	To xylem fibre		To xylem vessel	To xylem fibre	
10	2	0	0	1	0	0
30	3	0	2	0	1	0
50	2	2	1	0	2	0
70-80	3	3	1	1	2	0
90-100	1	1	0	0	3	0

TABLE 5. Depth and availability of xylem elements in *M.sativa* ($\bar{x} \pm SE$). Sampling and statistical procedures as in Table 1.

Distance below terminal bud (cm)	Depth of xylem elements (mm)		Availability of xylem elements	
	Minimum	Median	Number/mm	% Circumference
10	0.204 $\pm$ 0.013 ^a	0.243 $\pm$ 0.013 ^a	19 $\pm$ 1 ^a	43.6 $\pm$ 2.6 ^a
30	0.242 $\pm$ 0.010 ^{ab}	0.381 $\pm$ 0.015 ^b	12 $\pm$ 1 ^b	31.1 $\pm$ 1.2 ^b
50	0.253 $\pm$ 0.008 ^b	0.433 $\pm$ 0.016 ^{bd}	10 $\pm$ 1 ^{bc}	21.2 $\pm$ 0.9 ^c
70	0.304 $\pm$ 0.023 ^b	0.561 $\pm$ 0.051 ^c	7 $\pm$ 1 ^c	20.9 $\pm$ 1.3 ^c
90	0.286 $\pm$ 0.004 ^b	0.522 $\pm$ 0.026 ^d	9 $\pm$ 1 ^{bc}	21.3 $\pm$ 0.9 ^{2b}

increasing distance from the apex and the presence of trichomes in regions of hard tissues. On *M.sativa*, restricted feeding by the fifth instar lower on the stem was associated with tissue hardness and reduction in the availability of xylem vessels in the penetrable region of the stem. Increased tissue hardness in both host species was associated with an increase in the amount of lignification of tissues at increasing distances from the terminal bud, but the specific tissues impeding stylet penetration differed in the two hosts. In *A.margaritacea* the lignified bundle cap and interfascicular parenchyma provided resistance. In *M.sativa* the lignified xylem fibres provided resistance. Additional minor sources of resistance were the lignified xylem fibres of pearly everlasting and the collenchyma in the bundle cap of alfalfa.

Homoptera that penetrate plant tissue using thin, flexible stylets and digestive enzymes, Aphidae (Staniland, 1924; Knight & Alston, 1974) and Pseudococcidae (Entwistle & Longworth, 1963), have difficulty penetrating lignified and other hard tissues; this difficulty explains a portion of host resistance to these insects. This study showed that the Cercopidae, which have more robust stylets and penetrate intracellularly without using enzymes,

were also prevented from reaching feeding sites by lignified tissue.

Our finding that trichomes on *A.margaritacea* were a significant barrier to spittlebug feeding agrees with earlier evidence of trichome resistance to stylet feeding insects (Painter, 1951; Levin, 1973; Webster, 1975). However, the mechanism of trichome resistance apparently differs on hard and soft areas of the stem. On soft apical stem tissue, young nymphs experience difficulty when the trichomes prevent the rostrum from contacting the epidermis and receiving the stimuli to begin stylet penetration (Hoffman & McEvoy, 1985). The larger fourth and fifth instars overcome this resistance because of their longer rostra. Further down on the stem, trichomes apparently prevent the older nymphs from achieving the grasp of the stem required to generate stylet forces sufficient to penetrate hard tissue. Spittlebugs sectioned on the stem had their legs above the trichome mat and appeared unable to grasp the stem directly (Hoffman, 1983).

We estimated that maximum depth of penetration represents about 82% of the mean stylet length. If this is so, then we conclude that the depth of the xylem elements was not a barrier on the hosts studied. However, the

longer stylet length in proportion to body size in the young instars of *P. spumarius* (Hoffman, 1983), leafhoppers (Pollard, 1968) and aphids (Mittler, 1954) suggests that the depth of the tissues below the surface may have contributed to the evolution of longer stylets in juvenile stages of sap feeders.

The ability of nymphs to penetrate through trichomes and hard tissue increased with body size. Size dependent differences in the ability to overcome mechanical barriers can result in a larger proportion of the plant being available to larger nymphs (Halkka *et al.*, 1977; Hoffman, 1983; McEvoy, 1985). This may allow a wider choice of food and habitat and relax competition within and between species.

Since mechanical barriers inside the stem were not manipulated experimentally in our study, there remains the possibility that other factors correlated with tissue hardness could account for the decline in feeding, the increased frequency of stylet sheaths terminating in lignified tissue, and the variation in the effect of trichomes with increasing DBTB, as well as an increase in the range of sites exploited with increase in instar. The histological characters we studied are probably correlated with biochemical factors studied by Horsfield (1977). He showed that amino acid concentrations in leaves on *Xanthium strumarium* plants decline with distance from the apex, and survivorship and feeding rates in *P. spumarius* are positively correlated with amino acid concentration. He also showed by manipulative experiments that a certain concentration of amino acids in the xylem sap is necessary for spittlebugs to settle at a feeding site. The influences of anatomical and nutritional factors might be separated experimentally by increasing amino acid concentration in parts of the plant that seem to exhibit anatomical barriers to feeding to see if these are then overcome, and/or select plant species in which anatomical gradients and biochemical gradients are not confounded. Our experimental host, alfalfa, may be an appropriate choice, since under field conditions the concentration of reduced nitrogen declines as the sap ascends the stem (G. H. Heichel, personal communication). In any event, in tissues where access to the xylem is not restricted by mechanical barriers, we expect selection of feeding sites based on variation in food quality as Horsfield (1977) observed.

This research demonstrates there are important mechanical limitations on food resources available to spittlebugs, and these limitations are a principal cause of restricted distribution on the host plants studied. In order to feed, a spittlebug must generate forces at the stylets that exceed the resistance offered by plant tissues. The stylet forces increase with spittlebug stage and decrease due to interference from trichomes, while plant resistance increases with distance from the terminal meristem. In order to produce spittle, the frothy secretion which surrounds and protects the nymph from enemies and physical risks (Whittaker, 1970), the nymph must feed. Thus mechanical limitations on feeding have a profound influence on the nymphs's interactions with other organisms and the physical environment.

Acknowledgments

We wish to thank R. E. Berry, C. S. Cox, J. H. Lawton, J. Parke, F. R. Rickson and two anonymous reviewers for improvements in the manuscript made possible by their comments. We thank F. R. Rickson for the use of his laboratory for anatomical studies. This is Oregon State University Agricultural Experiment Station Technical Paper No. 7493.

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Accepted 22 April 1985

Appendix

Regression coefficients and their standard errors for logistic regressions referred to in figure captions.

Model	Term	Coefficient	Standard Error	χ^2	P
Fig 2 Instars (1–5) on stems of <i>A. margaritacea</i>	INSTAR	3.564	1.015	75.370	<0.0005
	TRICHOME	−10.255	3.187	70.332	<0.0005
	CONSTANT	−0.99	0.000		
Fig. 3(a) Fourth instar on <i>A. margaritacea</i>	CONTROL	−4.924	0.000	8.52	0.0035
	DBTB	−0.130	0.041	10.636	0.001
	TRICHOME	−0.538	0.21	6.884	0.009
	D×T			0.01	0.911
	CONSTANT	7.11	0.713		
Fig. 3(b) Fifth instar on <i>A. margaritacea</i>	CONTROL	−4.296	0.000	3.62	0.057
	DBTB	−0.129	0.033	44.91	<0.0005
	TRICHOME	−2.471	1.248	11.058	0.001
	D×T	0.052	0.033	3.291	0.07
	CONSTANT	9.775	1.248		
Fig. 3(c) Fifth instar on <i>M. sativa</i>	DBTB	−0.053	0.026	7.294	0.007
	CONSTANT	6.404	2.136		

EL DAÑO ECONÓMICO DEL SALIVAZO DE LOS PASTOS EN COLOMBIA: UNA PRIMERA APROXIMACIÓN DEL IMPACTO SOBRE LA PRODUCCIÓN ANIMAL EN *BRACHIARIA DECUMBENS*

manuscrito en preparación

FEDERICO HOLMANN¹, DANIEL PECK² Y CARLOS LASCANO²

¹Centro Internacional de Agricultura Tropical (CIAT) e Instituto Internacional de Investigación en Ganadería (ILRI) Apartado Aéreo 6713, Cali, Colombia

²CIAT, Apartado Aéreo 6713, Cali, Colombia

Resumen. El objetivo fue cuantificar el daño económico como resultado de la reducción en producción de leche y carne con tres distintos grados de infestación de salivazo utilizando datos obtenidos en Brasil de la especie *Notozulia entreriana* (10, 25, y 50 individuos/m²) con tres proporciones del área en pasturas infestada (25%, 50%, y 100%) con animales pastoreando *Brachiaria decumbens* utilizando como herramienta de análisis un modelo de simulación. Se utilizó como referencia una finca de 100 ha en un sistema de producción de doble propósito localizado en dos ecosistemas contrastantes: (1) trópico seco, con una época de lluvias bien definida de 6 meses, representativa de la costa norte de Colombia (ie., departamentos de Atlántico, Bolívar, Cesar, Córdoba, Guajira, Magdalena y Sucre), y (2) trópico húmedo, con una distribución uniforme de lluvias a través del año, representativa de áreas de márgenes de bosque (ie., departamentos de Caquetá, Putumayo y Chocó). Los parámetros técnicos del hato de doble propósito en ambos sitios así como también la productividad promedio del *B. decumbens* fueron representativas de las condiciones de manejo del trópico húmedo y seco. Comparando el efecto del salivazo contra una pastura sana, éste redujo la carga animal y la productividad de leche y carne por hectárea 9%-34% con un nivel bajo de infestación, 38%-49% con un nivel medio de infestación, y 53%-65% con un nivel de infestación alto. El impacto del salivazo sobre los costos de producción de leche y carne incrementó los costos 3%-12% con un nivel bajo de infestación contra los costos de una pastura sana. Asimismo, este costo se incrementó 18%-29% con un nivel mediano de infestación, y 36%-54% con niveles altos. Debido a los efectos del salivazo sobre la reducción en la carga animal y producción de leche y carne, el ingreso neto por hectárea por año se disminuyó significativamente 19%-69% con un nivel bajo de infestación, 78%-100% con un nivel mediano de infestación, y 106%-128% con niveles altos. El daño económico llevado a escalas regionales varió \$7-25 millones de dólares por año en las 1,140,000 ha de pasto susceptibles al salivazo en el trópico húmedo y \$33-118 millones de dólares en las 4,720,000 ha de pasto susceptibles al salivazo en el trópico seco con un nivel de infestación moderadamente bajo. Este costo, con un nivel mediano de infestación, se incrementó \$28-36 millones de dólares en el trópico húmedo y \$132-175 millones en el trópico seco. Finalmente, con niveles altos de infestación de salivazo la reducción a nivel regional en los ingresos netos de los productores ascendió a \$39-47 millones de dólares para el trópico húmedo y \$228-273 millones de dólares para el trópico seco. La inversión estimada para el desarrollo de variedades de pasto resistentes al salivazo y adaptadas a suelos de baja a mediana fertilidad es del orden de los USD 6 millones de dólares con un horizonte de 12 años. Esta inversión, comparada con el daño económico que el salivazo causa en Colombia, es baja. Por lo tanto, existe un gran incentivo económico para que gremios de productores inviertan en mejoramiento varietal mediante contratos con instituciones de investigación con capacidad para el desarrollo exitoso de este producto.

Introducción

La ganadería en América tropical emplea sistemas extensivos de producción que dependen de las gramíneas forrajeras para la producción de carne y leche. Entre las gramíneas mas importantes se encuentran varias especies del género *Brachiaria* (Trin.) Griseb., en especial *B. decumbens* Stapf cv. Basilisk. Su introducción, principalmente en las sabanas neotropicales, ha aumentado la capacidad de

carga en tierras ocupadas anteriormente por gramíneas nativas de baja productividad (Lascano, xxxx).

Brachiaria decumbens cv. Basilisk es la especie de pasto mas difundida en América tropical con un estimado de 40 millones de ha, la mayoría de estas en Brasil, Colombia y Venezuela (Pizarro et al., 1998). La gran adopción de este cultivar se debe a que se adapta bien a suelos ácidos e infértiles y que forma una pastura agresiva, de alto rendimiento, que

resiste al pastoreo intensivo y el pisoteo de los animales (Keller-Grein et al., 1998). Asimismo, es una gramínea palatable de buena calidad nutricional y los animales que la consumen presentan buen desempeño. Sin embargo, su susceptibilidad al salivazo o mión de los pastos (Homoptera: Cercopidae) reduce su establecimiento y adopción en áreas en que esta plaga es importante como en las sabanas del neotrópico (Keller-Grein et al., 1998).

El salivazo es considerado como la plaga más dañina en las pasturas de América tropical por su amplia distribución y capacidad de rebrote. Se reportan docenas de especies en este complejo de insectos nativos que atacan gramíneas cultivadas desde el sur de Estados Unidos hasta el norte de Argentina. Algunas especies son plagas importantes de caña de azúcar (Fewkes, 1969) y de otras gramíneas cultivadas como arroz, sorgo, maíz, y césped (Nilakhe, 1985; Souza y Nilakhe, 1985; Braman y Pendley, 1993).

Tanto las ninfas como los adultos del salivazo se alimentan principalmente del xilema del huésped (Thompson, 1994). Los adultos, en particular, causan una respuesta fitotóxica por parte del huésped susceptible debido a ciertos componentes de la saliva (Byers y Wells, 1966; Valério et al., 1988). El resultado es una interferencia en la actividad fotosintética de la planta produciendo lesiones necróticas que se propagan longitudinalmente hacia el ápice de la hoja. Si ocurre un ataque severo, toda la parte aérea de la planta da la impresión de estar seca y muerta, reduciendo significativamente la producción de materia seca, digestibilidad, y calidad del forraje, disminuyendo así la carga animal y la producción de leche y carne (Valerio y Nakano, 1988 y 1989). Además del daño de los adultos, la capacidad alimenticia de las ninfas causa estrés hídrico y pérdidas de biomasa (Silva, 1982; Barrientos et al., 1988). De esta manera el impacto agregado de las ninfas y los adultos disminuye la persistencia de los pastos mejorados y contribuye a la degradación ambiental (Taliaferro et al., 1967; Valério y Nakano, 1987; Hewitt, 1989).

La duración del ciclo de vida y el número de generaciones anuales dependen de la especie de salivazo y de las condiciones climáticas locales. En regiones húmedas es posible encontrar el salivazo durante todo el año, mientras que en regiones más secas, el período de infestación tiene la misma duración que la época de lluvias. *Aeneolamia reducta* (Lallemand) logra 6 generaciones al año en el trópico seco de la Costa Norte de Colombia a pesar de unos 4 meses de sequía al año (Peck et al., 1999). En el trópico húmedo del Piedemonte Amazónico de Colombia, donde no hay un período seco definido, no

hay sincronización poblacional y el salivazo ocurre durante todo el año.

Aunque es obvio que el salivazo ocasione un daño severo a las plantas huéspedes, la información sobre el impacto de la plaga en la producción animal a lo largo de toda la época de pastoreo es nula (Valerio, 1998). No conocemos de ningún estudio que tenga estimativos del daño económico regional basado en datos concretos, debido principalmente a que son escasos los estudios que han evaluado el impacto del salivazo sobre la planta huésped, la cual es fundamental para extrapolar el daño económico regional.

Objetivos

El objetivo de este estudio fue cuantificar el daño económico como resultado de la reducción en producción de leche y carne con distintos grados de infestación de salivazo en animales bajo pastoreo de *B. decumbens* utilizando un modelo de simulación.

Materiales y Métodos

Datos sobre calidad nutricional y producción de biomasa de *B. decumbens* bajo diferentes densidades del salivazo fueron obtenidos de Valério y Nakano (1988 y 1989). En sus estudios cuantificaron el impacto de 0, 25, 50 y 100 adultos de *Notozulia enteriana* (Berg) mantenidos a densidades constantes durante 10 días seguidos bajo jaulas de 1m² (Cuadro 1). Para representar un bajo nivel de infestación más real para nuestro estudio, se extrapó el impacto de 10 adultos/m² según un análisis de regresión. Se consideró 25 adultos como una infestación moderada y 50 adultos como una infestación alta. Se decidió no incluir el nivel de 100 adultos/m² evaluado por Valério y Nakano para simplificar los análisis y porque representa una presión que casi nunca se logra bajo las condiciones naturales del campo.

De Valério y Nakano (1988; 1989) se utilizó tres mediciones de calidad y producción: digestibilidad in vitro de la materia seca (DIVMS), proteína cruda (PC) y producción de biomasa (MS). Se sirvieron de estos datos para calcular la reducción en biomasa forrajera (ie. carga animal) y nutrientes disponibles (ie. energía digestible y proteína) para ganado pastoreando sobre *B. decumbens* según los diferentes niveles de infestación. Basado en estos resultados se estimó la pérdida en productividad de leche y carne.

Para estimar el daño económico causado por el salivazo se tomó como referencia una finca con un área de 100 ha de *B. decumbens* en un sistema de producción de doble propósito localizado en dos ecosistemas contrastantes. El ecosistema trópico

seco se caracteriza por una época de lluvias bien definida de 6 meses y es representativa de la costa norte de Colombia (ie., departamentos de Atlántico, Bolívar, Cesar, Córdoba, Guajira, Magdalena y Sucre). El ecosistema trópico húmedo se caracteriza por una distribución relativamente uniforme de lluvias a través del año y es representativa de áreas de márgenes de bosque (ie., departamentos de Caquetá, Putumayo y Chocó). Los parámetros técnicos del hato de doble propósito en ambos sitios se encuentran en el Cuadro 2 así como también la productividad promedio del *B. decumbens* bajo las condiciones de manejo del trópico húmedo y seco en el Cuadro 3.

Debido a que los ataques del salivazo ocurren durante la época de lluvias, en el trópico húmedo el impacto del salivazo es relativamente uniforme durante el año. Al contrario, en el trópico seco el insecto sobrevive la época seca como huevos diapáusicos así que la presencia de ninfas y adultos está limitado a la mitad del año. Por lo tanto, para el propósito de este análisis, se consideró que el daño económico del salivazo es uniforme durante todo el año en el trópico húmedo pero en el trópico seco se restringe a 6 meses, o la duración de la época lluviosa.

La tercera dimensión evaluada fue el área de la finca afectada por el salivazo. Se calculó el impacto con tres proporciones distintas de la finca bajo infestación permanente del salivazo: 25%, 50%, y la totalidad (100%) del área de pasturas en la finca infestada.

El Modelo de Simulación

Para calcular el daño económico, se alimentó a un modelo de simulación información sobre las tres variables: (1) nivel de infestación: bajo, mediano, alto; (2) área de la finca infestada: 0, 25, 50, 100%; y (3) ecosistema: trópico seco (infestación durante la mitad del año), trópico húmedo (infestación durante todo del año).

El modelo fue desarrollado inicialmente por el Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) y la Red Internacional de Sistemas de Producción Animal en América Latina (RISPAL), el cual fue luego expandido por el CIAT. Este modelo fue desarrollado en una hoja electrónica con el objetivo de evaluar en forma ex-ante los costos y beneficios del uso actual y potencial de la tierra y sus interacciones entre componentes tecnológicos y la productividad biológica (Holmann y Estrada, 1997).

De esta manera, el modelo predice en forma ex-ante la pérdida en productividad de leche y carne esperada según el nivel de infestación encontrado en una determinada pradera por un determinado período de tiempo. Esta reducción en la producción de leche

y carne es expresada en términos no solo de kilos de carne y leche, sino también en ingresos netos y costos de producción.

La estructura del modelo es flexible, para permitir al usuario modificaciones parciales o totales dependiendo de intereses particulares y capacidad analítica. La estructura del modelo cuenta con seis hojas electrónicas. En la Hoja A se presenta la información básica para la corrida del modelo; en la Hoja B la información para realizar los cálculos de producción animal; en la Hoja C la información para realizar los cálculos sobre producción de pasturas y árboles maderables; en la Hoja D información para hacer cálculos de producción de cultivos; en la Hoja E información para estimar los costos de amortización y la inversión en infraestructura y equipo y en la Hoja F la matriz de correlaciones de la programación lineal. Para realizar este análisis se utilizó como soporte lógico la hoja electrónica Microsoft Excel, versión 7.0 para Windows.

El modelo asume que la función objetivo de los productores es el aumento del ingreso neto anual, por tanto realiza todos sus cálculos de manera anual y supone que la empresa agropecuaria se encuentra en equilibrio, por tanto no aumentan sus inventarios a través del año.

Resultados

Los Cuadros 4 y 5 muestran el efecto de los distintos niveles de infestación de salivazo en el trópico húmedo y seco de Colombia expresados en cuatro parámetros de importancia económica: (1) carga animal (UA/ha); (2) productividad de leche y carne (kg/ha/año); (3) costo de producción de leche y carne (US\$/kg); y (4) ingreso neto (US\$/ha/año). La información contenida en los Cuadros 4 y 5 ha sido convertida en ocho gráficas para facilidad de comprensión.

Carga Animal

En ambos ecosistemas la carga animal se redujo drásticamente en la medida que el nivel de infestación de salivazo aumentó (Gráficas 1 y 2). Esta carga animal es el resultado no solo de una reducción significativa de biomasa disponible en la pastura (Cuadro 1) sino también de la pérdida de calidad del *B. decumbens* tanto en términos de proteína como de energía, ya que ambos efectos están ligados al nivel de infestación del salivazo. La carga animal sin infestación en el ecosistema de trópico húmedo es mayor que en el trópico seco (1.16 vs. 0.93 UA/ha) debido a que la precipitación es mayor y mas uniforme durante todo el año y por lo tanto, la producción de biomasa de cualquier pastura es mayor.

Así, la capacidad receptiva de la pradera se redujo entre 2% y 7% al pasar de una pastura sana (sin infestación) a un nivel bajo de infestación (0 a 10 individuos/m²), dependiendo del porcentaje del área de la finca infestada (ie., de 1.16 a 1.14-1.08 UA/ha para el caso del trópico húmedo y de 0.93 a 0.91-0.86 UA/ha para el trópico seco, Cuadros 4 y 5). La diferencia en cargas animales tanto en pasturas sanas como infestadas en ambos ecosistemas obedece a que la carga animal siempre es mayor en el trópico húmedo debido a una mayor precipitación anual y mejor distribución de las lluvias a través del año.

De igual manera, la carga animal se redujo en un 2% a 30% adicional cuando el nivel de infestación se incrementó de bajo a mediano (10 a 25 individuos/m²), dependiendo del porcentaje del área de la finca infestada. Al pasar de una infestación mediana a alta (25 a 50 individuos/m²), la carga animal se redujo en otro 5% a 26% adicional. Es decir, comparando la misma pastura sana vs. una con un nivel de infestación alto, la carga animal se redujo entre 97% y 102%, es decir, a la mitad (ie., 1.16 vs. 0.59 UA/ha en el trópico húmedo y 0.93 vs. 0.46 UA/ha en el trópico seco).

Producción de Leche y Carne

Debido a la reducción en la carga animal así como también a la disminución de la calidad nutritiva de la pastura, la producción de leche se redujo entre 2% y 8% por hectárea en ambos ecosistemas cuando las vacas pasaron de pastorear una pastura sana a otra con un nivel de infestación bajo (Gráficas 3 y 4; Cuadros 4 y 5).

Aunque en términos porcentuales la reducción en producción de leche fue similar en ambos ecosistemas, en términos absolutos la disminución en producción de leche fue mayor en el trópico seco de Colombia debido a que el genotipo animal encontrado en este ecosistema produce mas leche (ie., 1200 vs. 760 kg/l) y posee un peso adulto mayor (ie., 450 vs. 400 kg) que el genotipo comunmente encontrado en las márgenes de bosque del trópico húmedo colombiano (Duarte et al., 1999; Rivas y Holmann, 1999).

De la misma manera, la producción de leche se redujo en un 1% a 28% adicional al pasar el nivel de infestación de bajo a mediano y en 6% a 23% adicional al pasar de mediano a alto, dependiendo del porcentaje del área de la finca infestada. Comparando la pastura sana vs. la pastura altamente infestada, la producción de leche y carne se redujo entre 60% y 97% (ie., 390 vs. 197 kg leche/ha en el trópico húmedo y 529 vs. 265 kg leche/ha en el trópico seco).

El caso de la carne fue similar en términos porcentuales que la leche. Es decir, la reducción en

productividad de carne por hectárea fue proporcionalmente similar a la leche en ambos ecosistemas. Sin embargo, al contrario que la leche, la producción de carne por hectárea en términos absolutos fue mayor en el trópico húmedo que en el seco debido a que la oferta de nutrientes y consumo voluntario a través del año es mayor.

La estrategia de los productores en el trópico seco ha sido concentrar su producción de leche en la época de lluvias. Sin embargo, durante la época seca los animales pierden peso teniendo como resultado que, bajo los parámetros reportados en este estudio (Cuadros 2 y 3), la producción de carne es inferior al trópico húmedo.

Costo de Producción de Leche y Carne

Los efectos del salivazo sobre la reducción de la carga animal y producción de leche y carne tienen también un efecto directo sobre los costos de producción. Así, con un nivel de infestación bajo, los costos de producción tanto de leche como de carne se incrementaron entre 2% y 4%, dependiendo del porcentaje del área de la finca infestada (Gráficas 5 y 6; Cuadros 4 y 5).

De la misma manera, al pasar de un nivel de infestación bajo a mediano, el costo unitario de producción de leche y carne se incrementó adicionalmente entre 1% y 12% y al pasar de un nivel mediano a alto este costo aumentó adicionalmente entre 2% y 13%. Para concluir, el costo de producir leche y carne en una pastura altamente infestada de salivazo es 30% mayor que en la misma pastura sin salivazo.

Ingreso Neto

El parámetro que resume el daño económico del salivazo sobre la productividad de la pastura y sobre el hato en toda su magnitud es el ingreso neto por hectárea. Para ambos ecosistemas, el ingreso neto se redujo entre 3% y 16% al comparar los beneficios económicos de una pastura sana a una con un nivel de infestación bajo, dependiendo del porcentaje del área de la finca infestada (Gráficas 7 y 8, Cuadros 4 y 5). El cambio fue de \$32 a \$31-\$27/ha para el trópico húmedo y de \$42 a \$40-\$36/ha para el trópico seco.

Asimismo, al pasar de un nivel de infestación bajo a mediano el ingreso neto se redujo adicionalmente entre 3% y 65% según el porcentaje del área de la finca bajo infestación (ie., de \$27 a \$26-\$10/ha para el trópico húmedo y de \$36 a \$35-\$17/ha en el trópico seco). Por otro lado, con un nivel de infestación alto los ingresos netos se redujeron adicionalmente entre 17% y 100% (ie., de \$10 a \$7-\$0/ha para el trópico húmedo y de \$17 a \$14-\$5/ha en el trópico seco). El ingreso neto de

\$0/ha en el caso del trópico húmedo significa que el sistema de producción ya no es viable económicamente con el 100% de la finca bajo una infestación alto del salivazo (Cuadro 4).

Comparando una pastura sana contra la pastura altamente infestada, el ingreso neto se redujo entre la mitad y la sexta parte (ie., de \$32 a 0/ha/año en el trópico húmedo y de \$42 a \$5/ha/año en el trópico seco).

Una alternativa existente para controlar la población del salivazo en la pastura es la utilización de productos químicos como los clorpiritos (ej., Lorsban). Sin embargo, el costo del producto (\$16/ha) y el costo adicional de la mano de obra para aplicarlo (\$8.85/ha) reducirían el ingreso neto en \$24.85/ha, lo cual no es económicamente viable, pues el ingreso neto por hectárea en estos sistemas de producción varían entre \$32/ha/año y \$42/ha/año y no existe garantía que la pradera no será infestada nuevamente durante la época de lluvias.

Daño productivo y económico a nivel de ecosistemas

Para estimar el impacto del salivazo sobre la producción animal y su correspondiente daño económico es necesario extrapolar los resultados expresados a nivel de finca generados por el modelo de simulación a los ecosistemas analizados en este estudio.

Se calcula que en el trópico húmedo de Colombia (ie., departamentos de Caquetá, Putumayo y Chocó) existen aproximadamente 1.6 millones de cabezas de ganado vacuno que representan el 6.1% del hato nacional y el área en pasturas es aproximadamente 1.2 millones de ha (DANE, 1996). De esta área en pasturas se estima que el 95% se encuentra establecida con *B. decumbens* y *Homolepis aturensis* Kunth (Chase) ("guaduailla"), ambos susceptibles a ataques de salivazo (comunicación personal, John Miles, mejorador de forrajes, CIAT). Existen, entonces, 1.14 millones ha de pastos bajo el peligro permanente de infestación.

En el trópico seco de Colombia (ie., departamentos de Atlántico, Bolívar, Cesar, Córdoba, Guajira, Magdalena y Sucre) se estima una población bovina de 8.0 millones de cabezas que representan el 31.3% del hato nacional y el área en pasturas es aproximadamente de 5.9 millones de ha (DANE, 1996). De esta área en pasturas se estima que el 80% se encuentra establecida con *B. decumbens* y *Bothriochloa pertusa* (L.) A. Camus ("colosuana"), las cuales son susceptibles a ataques de salivazo (comunicación personal, John Miles, mejorador de forrajes, CIAT). Por lo tanto, en este ecosistema existen aproximadamente 4.72 millones de ha sujetos a infestación unos seis meses al año.

Con base en estas cifras, se estimó el daño económico para cada ecosistema del efecto del salivazo sobre la pérdida en producción de leche y carne expresada tanto en kilogramos de producto como en dólares (Cuadro 6).

A un nivel de infestación bajo, y dependiendo del porcentaje del área de la región infestada, la pérdida anual en producción de leche fue 8 - 34 millones de litros de leche fluida en el trópico húmedo y 47 - 189 millones de litros para la región del trópico seco. Para la producción de carne el valor de la pérdida fue 2-8 millones de kilos anuales para el trópico húmedo y 7-28 millones de kilos para el trópico seco. La sumatoria de la pérdida de carne y leche traducida en dólares implicó una reducción neta en los ingresos de los productores de \$1.4-5.7 millones de dólares anuales en el trópico húmedo y \$7.1-28.3 millones anuales en el trópico seco. Por lo tanto, el daño económico anual sumando las dos regiones y tomando como escenario el nivel bajo de infestación fue \$8.5-34 millones de dólares anuales.

La pérdida económica es aún mayor con el nivel de infestación mediano. Bajo este escenario la pérdida en producción de leche fue 37-150 millones de litros anuales en los márgenes de bosque y 212-845 millones de litros de leche en el trópico seco. De la misma manera, la pérdida en producción de carne ascendió 9-36 millones de kilos en el trópico húmedo y 33-137 millones de kilos de carne en el trópico seco. Este impacto traducido a valor monetario implicó una pérdida directa en el flujo de caja de los productores de \$7-25 millones de dólares anuales en el trópico húmedo y \$33-118 millones de dólares anuales en el trópico seco. Estas cifras sugieren que el daño potencial económico con un nivel mediano de infestación sumando las dos regiones es \$40-143 millones de dólares anuales.

La situación se torna aún mas dramática cuando se analiza el escenario de un nivel de infestación alto. En este ambiente, la pérdida anual en producción de leche fue 167-220 y 948-1246 millones de litros de leche para el trópico húmedo y seco, respectivamente. Por el lado de la carne las pérdidas fueron 41-54 y 151-198 millones de kilos en el trópico húmedo y seco, respectivamente. Por lo tanto, el daño económico bajo el escenario mas pesimista fue 28-36 millones de dólares por año en la región de trópico húmedo y 132-175 millones de dólares por año para el trópico seco. El saldo total de ambas regiones indica que el daño económico que puede causar el salivazo con un nivel alto de infestación es 161-211 millones de dólares anuales, dependiendo del porcentaje del área de la región bajo permanente infestación durante la época de lluvias. Este daño no incluye otras regiones del país como los llanos orientales donde existen áreas de pasturas con

variedades susceptibles al salivazo. Por lo tanto, el daño potencial reportado en este estudio es conservador.

Implicaciones para la Investigación

El daño económico causado por el salivazo reportado en este estudio es una primera aproximación de su posible impacto sobre los ingresos de los productores colombianos localizados en las regiones evaluadas. Este daño económico puede variar de acuerdo al nivel de infestación, el cual es distinto año a año debido a cambios que ocurren con los niveles de precipitación, así como con la frecuencia e intensidad de las lluvias.

Un supuesto importante de los resultados obtenidos en este estudio es el origen de los datos del impacto sobre la calidad de la planta y la producción de biomasa. Los estudios de Valério y Nakano (1988, 1989) son los más completos hasta la fecha pero tratan de solamente el salivazo *N. entreariana* sobre *B. decumbens*. En nuestro estudio estos datos se utilizaron para estimar el impacto de otras especies de salivazo sobre otras gramíneas forrajeras en Colombia.

Una cuantificación del daño de las especies más comunes en el trópico húmedo y seco de Colombia todavía no se ha llevado a cabo. Precisar los estimativos del impacto depende de estudios detallados, en la manera de Valério y Nakano (1988, 1989), con las varias combinaciones de especies de salivazo y gramíneas. Por ejemplo, la asociación más importante en la Costa Norte de Colombia es *A. reducta* sobre *B. pertusa*, en el Piedemonte Amazónica es *Aeneolamia varia* (F.) y *Zulia pubescens* (F.) sobre *Brachiaria* y en los Llanos Orientales es *A. varia* sobre *B. decumbens*. Hay 15 especies de 8 géneros de salivazo asociados con gramíneas en Colombia y el complejo varía según región. Esta diversidad taxonómica probablemente influiría en el impacto, pero el grado de variación es aún desconocida. Además, datos específicos sobre la biología y comportamiento de la mayoría de estas especies no existen. Estudios para determinar la cuantificación del daño y de bioecología son sumamente importantes para precisar estimativos de impacto y para avanzar en el manejo del salivazo.

No hay resultados sobre el impacto de ninfas que se puede extrapolar a nivel de campo. Aunque probablemente el daño ocasionado por este estado de vida no supera lo de los adultos, es significativo y debe ser incluido. Por esta razón, los resultados obtenidos en este estudio se consideran conservadores ya que no incluyeron el daño económico y productivo causado por las ninfas del salivazo.

Además de tomar en cuenta la biología e impacto específico de las asociaciones salivazo/forraje presente en las diferentes regiones de Colombia, estimar el daño económico dependerá de la ecología del insecto. Con este estudio no se intentó relacionar el modelo de simulación con poblaciones reales a nivel del campo. Un próximo paso debe ser la comparación de estos resultados basados en niveles de infestación sujetos a niveles reales de abundancia del insecto a nivel de campo. Para lograr este objetivo se requiere de estudios de dinámica poblacional que ofrecen alta resolución (muestreos frecuentes de todos los estados de vida), así como también de información sobre la variabilidad a nivel de finca, a nivel de ecosistema (regiones diferentes), y a nivel del tiempo (muestreos durante varios años) (Peck 1999).

Actualmente existen en el mercado especies y variedades de pastos que demuestran cierta resistencia al salivazo aunque parece que este nivel varía según la especie de salivazo. Sin embargo, bajo ciertas circunstancias *Panicum maximum* Jacq., *Andropogon gayanus* Kunth, *Brachiaria brizantha* (Hochst. Ex A. Rich.) Stapf, y *Brachiaria dictyoneura* (Fig. & De Not.) Stapf ofrecen alternativas. Sin embargo, estas especies de pasto requieren suelos de mediana a alta fertilidad y un manejo adecuado que incluya la fertilización nitrogenada o la asociación con leguminosas para evitar la degradación de la pastura. Estas características limitan en gran medida los nichos ecológicos de estos pastos. Por lo tanto, existe una gran necesidad para desarrollar variedades de pasto resistentes al salivazo y a la vez adaptados a suelos de baja a mediana fertilidad.

La inversión necesaria para el financiamiento de un programa para el desarrollo de nuevas variedades de pasto resistentes al salivazo y adaptadas a estas condiciones se estima que cuesta alrededor de US\$ 500,000 anuales por un período de 12 años (comunicación personal, John Miles, mejorador de forrajes, CIAT). Es decir, el costo total estimado para el mejoramiento varietal de este pasto validado y entregado a los productores es de US\$ 6 millones de dólares que equivale al 70% del costo económico a los productores de un solo año con el nivel bajo de infestación y área de la región infestada mas baja.

Esta cifra sugiere que existe un gran incentivo por parte de gremios de productores para invertir en institutos de investigación con capacidad tecnológica para el desarrollo de variedades de pastos resistentes a salivazo.

Conclusiones

Los resultados obtenidos del impacto del salivazo sobre fincas con parámetros de productividad animal representativas del trópico seco y húmedo de Colombia (representado por la costa norte y los márgenes de bosque) y alimentadas al modelo de simulación sugieren las siguientes conclusiones:

- 1 Comparando el efecto del salivazo contra una pastura sana, ésta redujo la carga animal y la productividad de leche y carne por ha 2%-8% con un nivel bajo de infestación, 9%-34% con un nivel medio, y 38%-50% con un nivel de infestación alto. Esta situación ocurrió en las mismas proporciones tanto en el trópico húmedo como en el trópico seco. Sin embargo, la diferencia radicó en que el daño sobre la pastura en el trópico húmedo se prolongó durante todo el año debido a que el régimen de lluvias es permanente mientras que en el trópico seco el efecto del salivazo se limitó a los 6 meses que dura la época de lluvias.
- 2 El impacto del salivazo sobre los costos de producción de leche y carne fue negativo, pues incrementó los costos 1%-3% con un nivel bajo de infestación contra los costos de una pastura sana. Asimismo, este costo se incrementó 4%-15% cuando el nivel de infestación mediano, y 19% -29% con niveles altos de infestación.
- 3 Debido a los efectos del salivazo sobre la reducción en la carga animal y producción de leche y carne, el ingreso neto por ha por año se disminuyó significativamente. Así, el ingreso neto se redujo 3%-16% con un nivel bajo de infestación comparado con una pastura sana. Al incrementar el nivel de infestación a niveles moderadamente altos, este ingreso neto se redujo 19%-68%, y al llegar a niveles altos de infestación, el ingreso se redujo 78%-100%.
- 4 El daño económico llevado a escalas regionales se estimó en una pérdida que varió entre \$1.4 a 5.7 millones de dólares por año en las 1,140,000 ha de pasto susceptibles al salivazo en el trópico húmedo y entre \$7 a 28 millones de dólares en las 4,720,000 ha de pasto susceptibles al salivazo en el trópico seco con un nivel de infestación bajo. Este costo, con un nivel mediano de infestación, se incrementó \$7-25 millones de dólares en el trópico húmedo y \$33-118 millones en el trópico seco. Finalmente, con niveles altos de infestación de salivazo la reducción a nivel regional en los ingresos netos de los productores

ascendió a \$28-36 millones de dólares para el trópico húmedo y \$132-175 millones de dólares para el trópico seco.

- 5 Llegar a un estimativo del daño económico más preciso depende de (a) nueva información sobre la biología y comportamiento de las especies de salivazo aún desconocidas, (b) nuevos estudios para cuantificar el impacto de las combinaciones de especies de salivazo y gramíneas forrajeras relevantes en la región de estudio, tanto para ninfas como para adultos y (c) estudios detallados de dinámica poblacional para relacionar la circunstancias reales de campo con los resultados del modelo de simulación, especialmente para precisar la variación espacial, estacional y entre años en la infestación del insecto
- 6 La inversión estimada para el desarrollo de variedades de pasto resistentes al salivazo y adaptadas a suelos de baja a mediana fertilidad es del orden de los USD 6 millones de dólares con un horizonte de 12 años. Esta inversión, comparada con el daño económico que el salivazo causa en Colombia, es baja. Por lo tanto, existe un gran incentivo económico para que gremios de productores inviertan en mejoramiento varietal mediante contratos con instituciones de investigación con capacidad para el desarrollo exitoso de este producto.

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Cuadro 1. Digestibilidad in vitro de la materia seca (DIVMS), peso seco, y proteína cruda (PC) de *Brachiaria decumbens* según distintas densidades de población de adultos de *Notozulia entreriana* en Brasil.

Adultos/m ²	Digestibilidad (%)	Peso Seco (g/m ²)	Proteína Cruda (%)
0	65.9	66.5	10.3
10	64.9	61.9	9.8
25	59.5	44.1	8.3
50	51.2	33.7	7.2

Fuente: Adaptado de Valério y Nakano (1988; 1989)

Cuadro 2. Parámetros productivos del *Brachiaria decumbens* bajo condiciones de manejo en el trópico húmedo (Caquetá) y trópico seco (Costa Norte) en Colombia.

Atributo	Trópico Húmedo ¹	Trópico Seco ²
Producción de biomasa (kg MS/ha)³		
- Época de lluvias	5300 – 8000	2600 – 4000
- Época seca ⁴	NA	260 – 400
Digestibilidad (%)³		
- Época de lluvias	60 - 66	60 – 66
- Época seca	NA	45
Proteína Cruda (%)³		
- Época de lluvias	8 – 10	8 – 10
- Época seca	NA	3
Traspaso biomasa de época de lluvias a seca (kg MS)⁵	NA	650 – 1000
Pérdidas por pisoteo (%)		
- Época de lluvias	30	30
- Época seca	NA	20
Uso de mano de obra (jornales/ha/año)	7	7
Costo de establecimiento (US\$/ha)	294	294
Consumo voluntario animal (% PV)		
- Época de lluvias	2.5	2.5
- Época seca	NA	2.0

¹ Rivas y Holmann (1999)

² Duarte et al (1999)

³ Tomado del Cuadro 1 de acuerdo a los diferentes grados de infestación

⁴ Equivalente al 10% de la producción de biomasa de la época de lluvias

⁵ Equivalente al 25% de la producción de biomasa de la época de lluvias

Cuadro 3. Parámetros de productividad animal de hatos de doble propósito bajo las condiciones de manejo del trópico húmedo (Caquetá) y trópico seco (Costa Norte) en Colombia.

Atributo	Trópico Húmedo ¹	Trópico Seco ²
Tasa de natalidad (%)	65	70
Reemplazo anual (%)	15	15
Carga animal (UA/ha)	1.16	0.93
Producción de leche (kg/lactancia)	760	1200
Duración de lactancia (días)	240	240
Precio de leche (US\$/kg) ³	0.16	0.16
Uso de mano de obra (jornales/vaca/año)	5	5
Peso adulto (kg)	400	450
Precio por jornal (US\$/día) ⁴	8.85	8.85
Valor comercial de animales (US\$)		
- Vaca en ordeño (400 kg)	320	320
- Vaca de desecho (350 kg)	240	240
- Ternero destetado (110 kg)	95	95

¹ Rivas y Holmann (1999)² Duarte et al (1999)³ Estimado en \$300/kg a una tasa de cambio de \$1,900 por dólar.⁴ Estimado en \$18,600/día incluyendo el 42.7% de prestaciones sociales.

Cuadro 4. Impacto biológico y económico de distintos niveles de infestación de salivazo y diferentes porcentajes del área de la finca bajo infestación en un sistema de producción de doble propósito en el trópico húmedo de Colombia.

Nivel y proporción de área infestada de salivazo	Carga animal (UA/ha)	Producción de leche ¹ (kg/ha/año)	Producción de carne ¹ (kg/ha/año)	Costo de producción de leche (\$/kg)	Costo de producción de carne (\$/kg)	Ingreso neto (\$/ha/año)
No infestación	1.16	390	95	0.123	0.61	32
10 individuos/m ²						
- 25%	1.14	382	94	0.124	0.62	31
- 50%	1.12	375	92	0.125	0.62	30
- 100%	1.08	360	88	0.126	0.63	27
25 individuos/m ²						
- 25%	1.06	357	87	0.128	0.63	26
- 50%	0.96	324	79	0.133	0.66	21
- 100%	0.76	258	63	0.142	0.70	10
50 individuos/m ²						
- 25%	0.72	243	59	0.146	0.72	7
- 50%	0.67	228	55	0.150	0.75	5
- 100%	0.59	197	48	0.159	0.79	0

¹ Kilos de leche fluída y kilos de carne en pie (peso vivo)

Cuadro 5. Impacto biológico y económico de distintos niveles de infestación de salivazo y diferentes porcentajes del área de la finca bajo infestación en un sistema de producción de doble propósito en el trópico seco de Colombia.

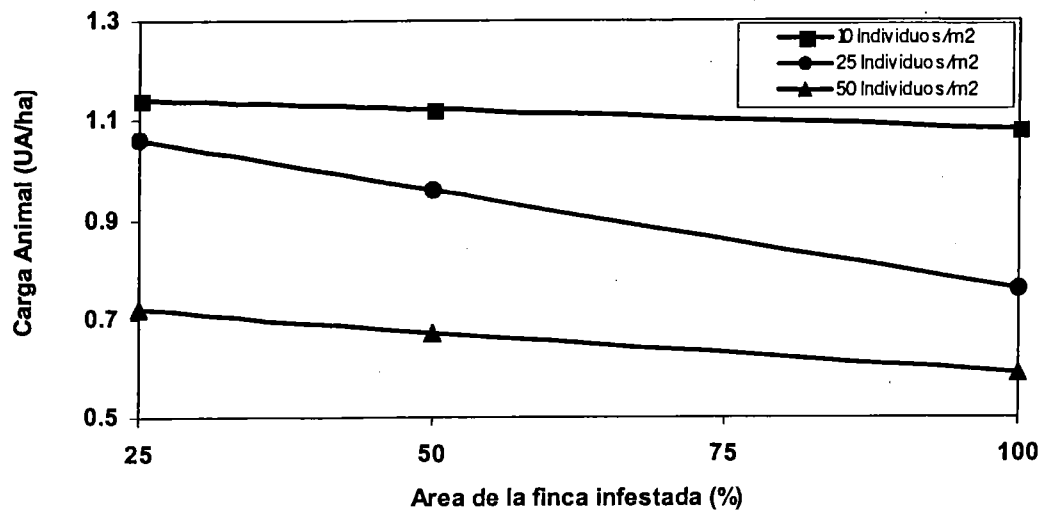
Nivel y proporción de área infestada de salivazo	Carga animal (UA/ha)	Producción de leche ¹ (kg/ha/año)	Producción de carne ¹ (kg/ha/año)	Costo de producción de leche (\$/kg)	Costo de producción de carne (\$/kg)	Ingreso neto (\$/ha/año)
No infestación	0.93	529	84	0.116	0.57	42
10 individuos/m ²						
- 25%	0.91	519	82	0.116	0.57	40
- 50%	0.90	509	81	0.117	0.58	39
- 100%	0.86	489	78	0.119	0.59	36
25 individuos/m ²						
- 25%	0.85	484	77	0.120	0.59	35
- 50%	0.76	439	70	0.125	0.62	29
- 100%	0.62	350	55	0.133	0.66	17
50 individuos/m ²						
- 25%	0.57	328	52	0.137	0.68	14
- 50%	0.53	307	49	0.142	0.70	11
- 100%	0.46	265	42	0.150	0.74	5

¹ Kilos de leche fluida y kilos de carne en pie (peso vivo)

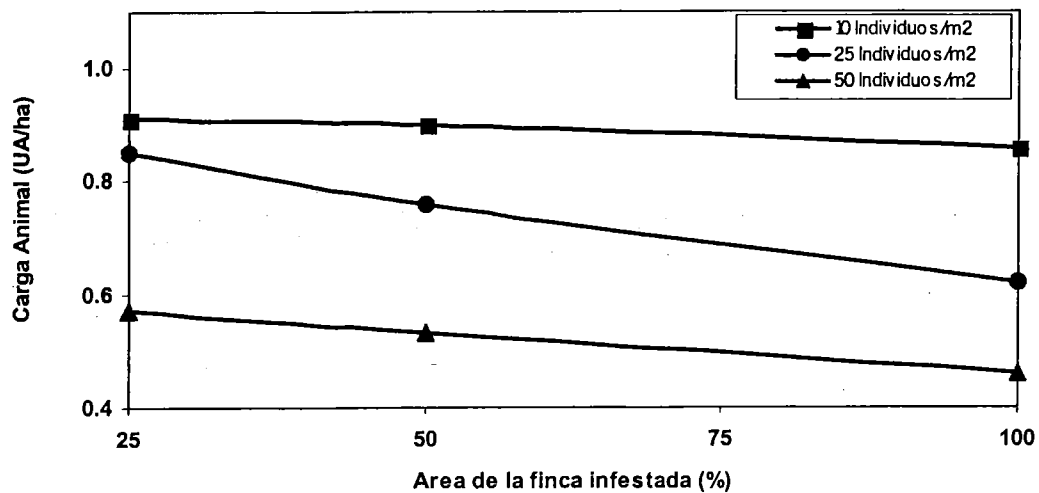
Cuadro 6. Daño económico a nivel de región del efecto del salivazo sobre la productividad de leche y carne en el trópico húmedo y seco de Colombia según distintos niveles de infestación y proporciones del área en pasturas infestadas.

Nivel y proporción de área infestada con salivazo	Pérdida en producción de leche (millones kg/año)		Pérdida en producción de carne (millones kg/año)		Pérdida Económica (millones US\$/año)	
	Trópico Húmedo	Trópico Seco	Trópico Húmedo	Trópico Seco	Trópico Húmedo	Trópico Seco
10 individuos/m ²						
- 25%	8.5	47.2	2.0	7.1	1.4	7.1
- 50%	17.1	94.4	4.0	14.2	2.9	14.2
- 100%	34.2	188.8	8.0	28.3	5.7	28.3
25 Individuos/m ²						
- 25%	37.6	212.4	9.1	33.0	6.8	33.0
- 50%	75.2	424.8	18.2	66.1	12.5	61.4
- 100%	150.5	844.9	36.5	136.9	25.1	118.0
50 Individuos/m ²						
- 25%	167.6	948.7	41.0	151.0	28.5	132.2
- 50%	184.7	1,047.8	45.6	165.2	30.8	146.3
- 100%	220.0	1,246.1	53.6	198.2	36.5	174.6

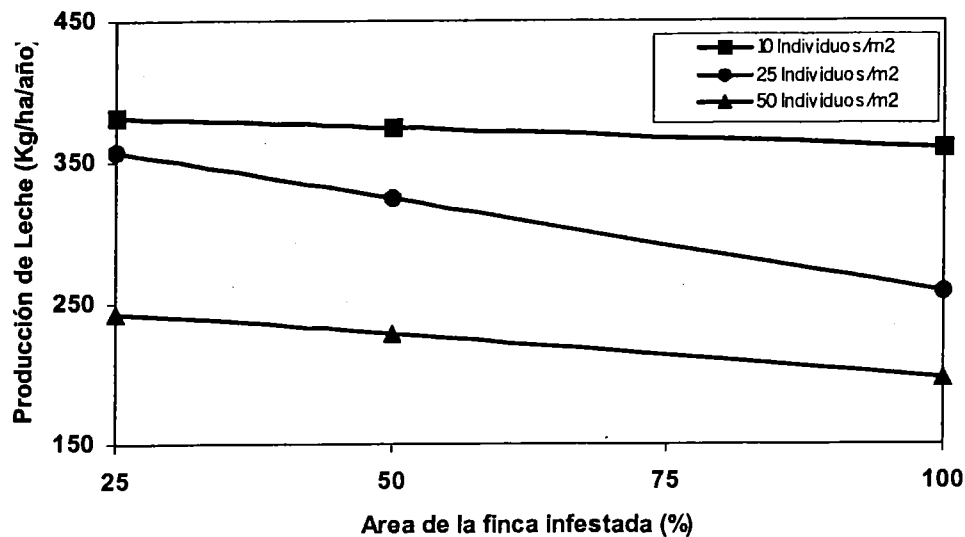
Gráfica 1. Efecto sobre la carga animal de distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico húmedo de Colombia



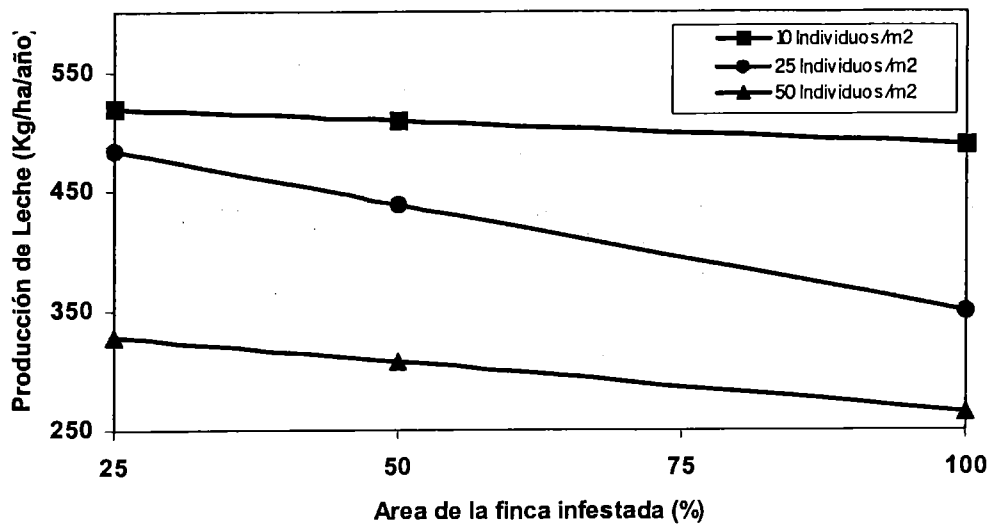
Gráfica 2. Efecto sobre la carga animal de distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico seco de Colombia



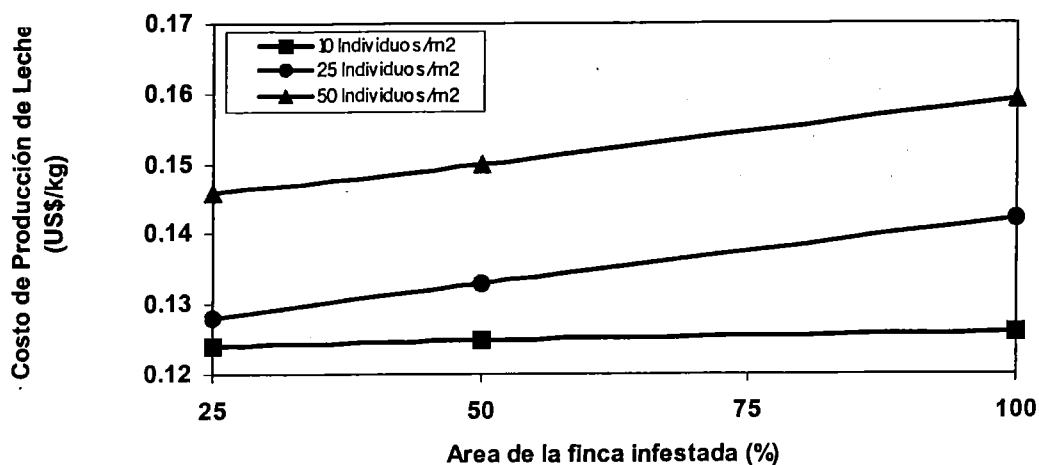
Gráfica 3. Efecto sobre la producción de leche según distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico húmedo de Colombia



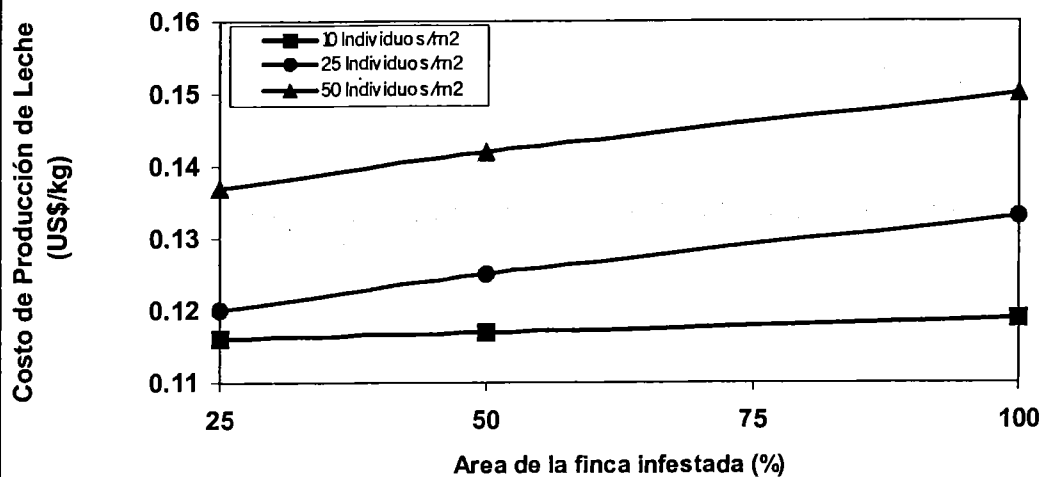
Gráfica 4. Efecto sobre la producción de leche según distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico seco de Colombia



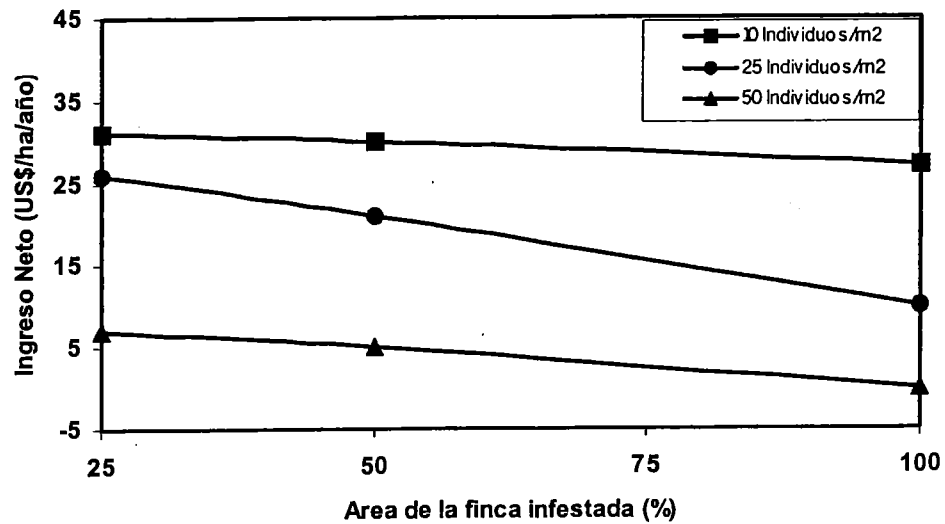
Gráfica 5. Incremento en el costo de producción de leche según distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico húmedo de Colombia



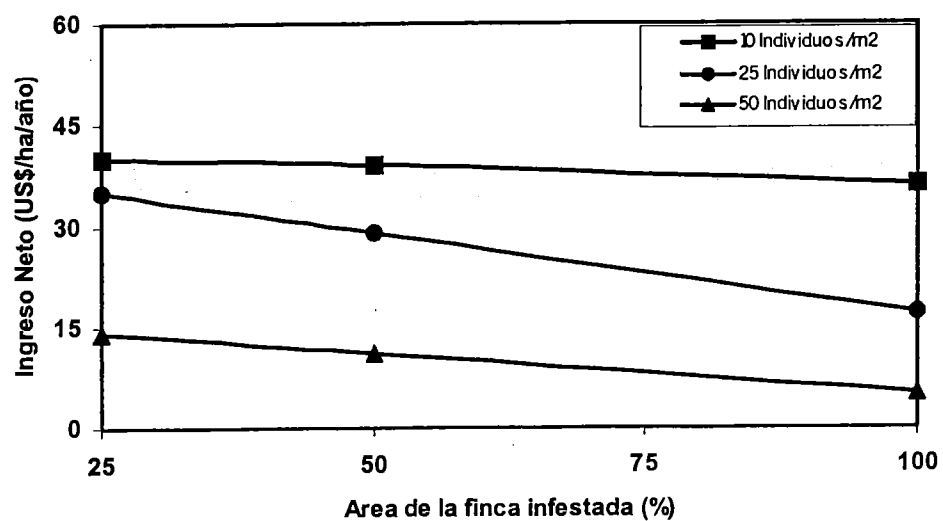
Gráfica 6. Incremento en el costo de producción de leche según distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico seco de Colombia



Gráfica 7. Impacto sobre el ingreso neto de distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico húmedo de Colombia



Gráfica 8. Impacto sobre el ingreso neto de distintos niveles de infestación de salivazo en pasturas de *B. decumbens* en el trópico seco de Colombia



Relationships between feeding of *Philaenus spumarius* (L.) and the amino acid concentration in the xylem sap

D. HORSFIELD Department of Biological Sciences, University of Lancaster

SUMMARY. 1. *P. spumarius* nymphs selected young, upper leaves of *Xanthium strumarium* plants, which have a relatively high amino acid concentration in the xylem sap.

2. Nymphs selected or rejected a host leaf as a feeding site after a test ingestion of plant sap.

3. Nymphs fed on detached leaves kept with their petioles in a solution of amino acids, in preference to leaves with petioles in a solution containing no amino acids.

4. Nymphs caged on leaves with relatively high amino acid concentrations in the xylem sap suffered a lower mortality after 7 days than nymphs caged on leaves with low amino acid concentrations in the xylem sap.

5. Mean excretory rate increased with the increase in the amino acid concentration in the xylem sap for third and fourth instar nymphs, and adults, but not in fifth instars.

Introduction

Philaenus spumarius (L.) (Homoptera: Cercopidae) has previously been shown to feed on the xylem vessel sap of its host plants (Wiegert, 1964; Horsfield, 1976). Nymphs produce the 'spittle', a foamy liquid formed by the introduction of bubbles from the air canal into the copious watery excrement. Nymphs remain static in their spittle masses, hence the feeding site on the plant is easy to see.

Weaver & King (1954) sought to explain the observed distribution of *P. spumarius* on its host plants by the availability of water within the plant. They state that spittlebugs are usually confined to the succulent young growth where sap can be obtained in large quantities, but make no suggestions as to which plant tissues the insect feeds on, and are presumably referring to the available

moisture within cells generally. However, unless the plant is wilting the xylem vessels provide a continuous source of water and nutrients, so the explanations offered by Weaver & King were considered inadequate to explain the distribution of the xylem feeding *P. spumarius* on its host plants.

Wiegert (1964) found that 98% of all organic matter in the xylem sap of tomato consisted of amino acids. Various authors (e.g. Bollard, 1960; van Die, 1958; Noguchi *et al.*, 1961; Pate & Wallace, 1964; Sheldrake & Northcote, 1968) had also demonstrated the importance of amino acids in the xylem sap. Much less information is available on other constituents that may have nutritional importance for *P. spumarius*. In contrast to the phloem, sugars are not a major constituent in the xylem sap.

In view of the probable importance of amino acids in the nutrition of *P. spumarius* observations were made to assess the relationship between site of spittle production (i.e. feeding site), nymphal mortality, nymphal

Correspondence: Dr D. Horsfield, Department of Biological Sciences, University of Lancaster, Lancaster LA1 4YQ.

and adult excretory rate and the concentration of amino acids in the xylem sap.

Materials and Methods

Extraction and analysis of xylem sap

Xylem sap was extracted from individual leaves of *Xanthium strumarium* L. by the pressure bomb technique of Scholander *et al.* (1966). Accumulated sap on the cut surface of the petiole or stem protruding from the chamber of the bomb was removed periodically with a Pasteur pipette. Sufficient sap for analysis could not be collected from leaves with a width (across the widest part) of less than about 2 cm.

The total free amino acid concentration in the xylem sap was determined by the ninhydrin method of Rosen (1957). This method is normally used for the quantitative determination of individual amino acids but can be applied to total amino acids provided that its limitations are appreciated. The method also determines the amount of ammonia present. Samples of xylem sap were therefore analysed for ammonia by the boric acid-HCl method of Conway (1962). Sap

from the whole shoots of eleven plants of *X.strumarium* gave a mean $\pm$ SE of $1.01 \pm 0.07 \mu\text{g}$ ammonium-N/ml. These small amounts of ammonia were discounted.

Laboratory observations of nymphs and adults

To observe nymphal mortality the host plants were kept uncovered under artificial light. When excrement was collected the plants were kept in sealed perspex cabinets in which the relative humidity was near to 100% to decrease the evaporation from the excrement collected. Keeping nymphs and adults at 100% RH was apparently not detrimental to their health and the excretory rate of adults kept at such high humidities was only slightly less than that of adults kept at ambient humidities.

To observe mortality and for excrement collection, nymphs and adults were confined in clip-cages to the underside of leaves with access to a large vein (Fig. 1). The felt pads on the lower half of the clip cage were omitted during excrement collection since they may have soaked up some of the excrement. Some excrement remained on the leaf surface, around the bodies of the nymphs and on the

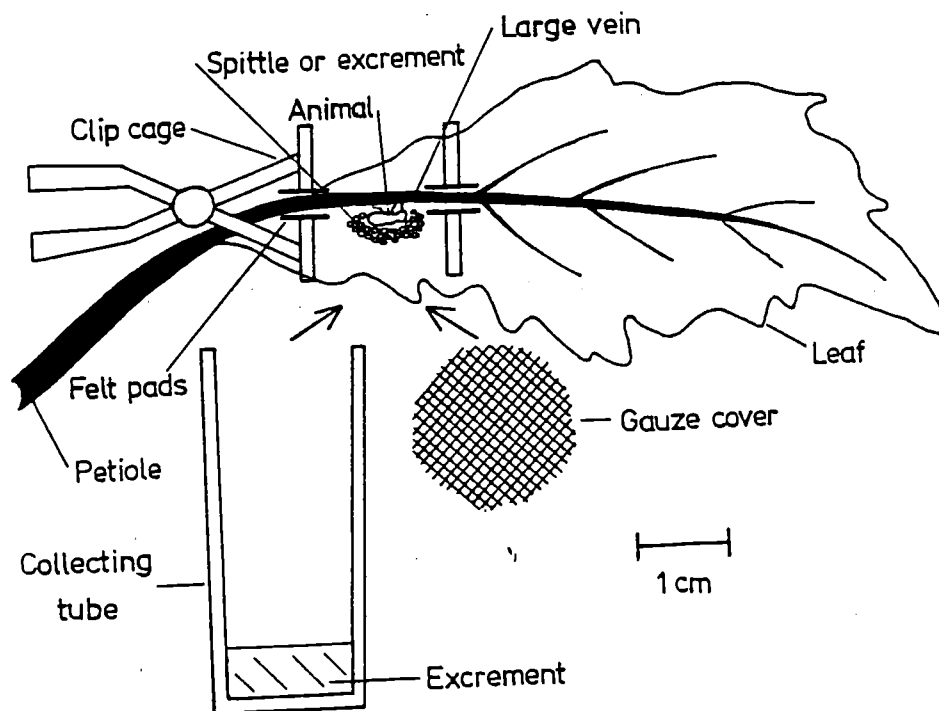


FIG. 1. Clip-cage to confine nymphs and adults of *P.spumarius* to leaves on the plant and detached leaves of *X.strumarium* in the laboratory. A gauze cover was attached to observe mortality or a tube was attached to collect excrement.

sides of the clip-cage. The amounts were generally too small to be collected by a Pasteur pipette. Most of the excrement ran down into the collecting tube; the amount of collected excrement was measured by weighing the collecting tube plus excrement, removing it, and reweighing the empty tube.

The composition and application of solutions to detached leaves

The composition of the amino acid solution applied to detached leaves of *X.strumarium* is given in Table 1. The concentrations of the amide and amino acids were ten times those given by van Die (1958) for the bleeding (xylem) sap of tomato. Only the five amide and amino acids with the highest concentrations were included. The mineral salts were determined approximately from analyses of K, Ca and PO_4 in *Vicia faba* L. xylem sap and from plant mineral salt nutrient solutions (Hewitt, 1966). The pH was the same as that given for xylem sap by Cheung & Marshall (1973), although the pH of *X.strumarium* xylem sap was later shown to be about 6.

To make up 1 litre of the solution in Table 1 the appropriate quantities of amino acids were dissolved in less than 500 ml of distilled water. The mineral salts were similarly dissolved in less than 500 ml of distilled water in the order given in Table 1, except for KOH which was added later. To make up the solution applied to the detached leaves the mineral salt solution was added to the amino acid solution and diluted with distilled water to a little less than 1 litre; 0.2 ml

of 50% KOH was then added to bring the pH up to 6.8 and the volume finally made up to 1 litre.

The mineral salt solution (control) was made up by dissolving the mineral salts as above but omitting the amino acids and making the solution up to 1 litre with distilled water. 0.2 ml of 50% KOH was still necessary to bring the pH up to 6.8.

To investigate its effect on adult excretory rate the total concentration of amino acids was varied from 0 to $4.03 \log \mu\text{M}$ while retaining the same proportions of individual amino acids as in Table 1.

Leaves were detached from the plant by cutting across the lower part of the petiole under water to prevent the formation of air-locks in the xylem vessels. Large, mature leaves (not normally selected for feeding by *P.spumarius*) were used. The cut end of the petiole was immersed in a small container with either the amino acid plus mineral salt solution (experimental) or the mineral salt solution alone (control). Feeding selection and spittle production by nymphs was observed on pairs of leaves, one with the experimental and the other with the control solution, placed in perspex cabinets. Movement from one leaf to another was possible since the nymphs were not confined. However, some nymphs after leaving one leaf failed to climb up on to the second leaf.

Results

The relationship between amino acid concentration in the xylem sap and sites of spittle production by nymphs feeding on Xanthium strumarium

Two *P.spumarius* nymphs were placed on each leaf of *X.strumarium* plants each having five to seven leaves with a maximum width greater than about 1 cm. After 2 days the leaves on which nymphs had formed spittle were noted. In a preliminary trial, two plants left for 6 and 7 days respectively, showed curling of the upper leaves on which the nymphs were feeding. Such symptoms were not visible after 2 days.

Xylem sap was extracted from all the leaves on a plant and the total free amino acid concentration in the sap from individual

TABLE 1. Composition of the solution applied to detached leaves of *X.strumarium*

L-Amino acids	$\log \mu\text{M}$
Glutamine	4.2
Valine	3.6
Leucine	3.4
Iso-leucine	3.4
Glutamic acid	2.8
Mineral salts	(g/l)
KH_2PO_4	0.5
$\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$	0.2
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.2
KOH	0.1
pH	6.8

TABLE 2. Amino acid concentrations in the xylem sap of *X.strumarium* leaves on which *P.spumarius* nymphs were and were not found feeding and producing spittle

Nymphal instars	No. of plants	Amino acid concentrations in xylem sap of leaves (log μM)			
		Nymphs with spittle		No spittle	
		Mean $\pm$ SE	n	Mean $\pm$ SE	n
First to fifth	28	3.08 $\pm$ 0.03	148	2.41 $\pm$ 0.03	74

leaves determined. The mean amino acid concentrations of the xylem sap from leaves on which nymphs had and had not produced spittle were calculated (Table 2). The amino acid concentration in the xylem sap increases in the upper, younger leaves (Fig. 2) and the nymphs settled on these. Pate *et al.* (1964) also found an increase in the organic nitrogen content (principally amides) in bleeding sap from successive petioles up the stem in tomato (*Lycopersicon esculentum* Mill.) and balsam (*Impatiens glandulifera* Royle).

Dried up, abandoned spittle masses were often found on some of the lower leaves, showing that nymphs had produced spittle initially on some of the lower leaves but after 2 days had moved to higher leaves. Thus, nymphs select upper leaves with relatively high amino acid concentrations in the xylem sap but they may not be responding to the

higher amino acid concentrations, but to other factors correlated with them.

The observations support Petty & White (1952) and Weaver & King (1954) who state that *P.spumarius* nymphs prefer the actively growing foliage of their host plants.

Observations on the mode of feeding site selection by *P.spumarius* nymphs on *X.strumarium* leaves

Selection or rejection of a feeding site on a plant may occur after the insect has ingested and 'sampled' the xylem sap, or external factors such as shape, colour, texture, smell, etc., of different parts of the plant may be important. Observations were made to determine whether or not ingestion of sap occurred prior to rejection or selection of plant leaves.

Third and fourth instar nymphs were removed from their spittles and partially dried on filter paper to remove liquid excrement, which may impede activity, surrounding the legs and body. They were then placed on either a bottom, middle or top leaf of *X.strumarium*.

The feeding activity of the nymphs was watched with the aid of a $\times 8$ hand lens and the results are presented in Table 3. Nymphs were considered to have inserted their stylets into plant tissue when they ceased to walk and moved their labium to a position at right angles to the plant surface. Montgomery & Arn (1974) used similar criteria to determine the initiation of probing when timing the probes of an aphid on an artificial diet enclosed in Parafilm.

After their introduction on to the surface of the leaf, nymphs generally moved around and made a few initial short stylet insertions. These short initial probes were of less than

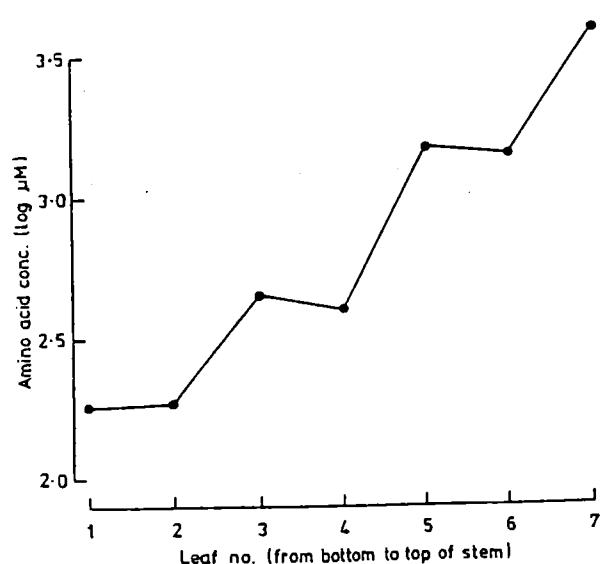


FIG. 2. Amino acid concentrations in the xylem sap of leaves on a representative plant of *X.strumarium*. Nymphs were found with spittle on leaves 5, 6 and 7.

TABLE 3. Stylet insertion, liquid and spittle production by *P.spumarius* nymphs on three leaves of *X.strumarium* plants

Leaf position	Amino acid concentration in xylem sap (log μM)	Instar	Total no. of nymphs	No. of nymphs which moved off the leaf					No. of nymphs which remained on the leaf after spittle produced
				After stylets not inserted into plant tissue	After stylets inserted into plant tissue				
					No liquid produced	Liquid produced	Spittle produced	Total	
Bottom	1.9	Fourth	17	2	4	9	1	16	1
Middle	2.5	Third, fourth	10	0	1	9	0	10	0
Top	3.1	Fourth	15	1	3	1	0	5	10

35 s duration and no liquid excrement was produced. Probes for longer than 35 s resulted in liquid appearing at the anus of the nymph in thirty-five out of thirty-eight instances.

The last two columns in Table 3 were tested for differences between the leaves by a χ^2 test. The difference between leaves 1 and 2 was not significant ($P = 0.6$), while the differences between leaves 1 and 3, and 2 and 3 were highly significant ($P < 0.001$). Nymphs therefore selected for preference the leaf with the highest concentration of amino acids in the xylem sap.

The principal differences in the number of nymphs which moved off the leaf between the bottom and middle and the top (Table 3) is in the number which inserted their stylets into plant tissue and produced liquid. Nymphs which inserted their stylets into plant tissue but produced no liquid probably failed to locate a xylem vessel.

Sixty-five per cent of nymphs which moved off the leaves did so after inserting their stylets into plant tissue and presumably ingesting sap to produce liquid excrement or spittle.

The general conclusion was that while some nymphs (on this case 35%) moved from the leaf without apparently ingesting sap, actual selection or rejection of a host leaf as a feeding site was based on a test ingestion of plant sap.

Selection for feeding and spittle production by P.spumarius nymphs on detached X.strumarium leaves

The amino acid plus mineral salt solution (Table 1) or the mineral salt solution alone were applied to detached leaves of *X.strumarium* so that nymphs were given the choice between leaves differing only in the concentration of amino acids in the xylem sap.

Three third, fourth or fifth instar nymphs were placed on the upper surface of each leaf and left 24 h before inspection. The leaves were examined for the presence of nymphs with spittle and for the presence of old, abandoned spittle masses. Any nymphs producing liquid excrement (i.e. without the bubbles of spittle) were also noted.

Table 4 gives the results of the experi-

TABLE 4. Feeding selection and spittle production by nymphs of *P.spumarius* on detached leaves of *X.strumarium* in relation to the amino acid concentration in the xylem sap

Amino acid concentration in the solution applied to detached leaf (log μM)	No. of leaves	Actual amino acid concentration in the xylem sap after 24 h (log μM) (mean $\pm$ SE)	No. of nymphs placed on each leaf at start	No. on each leaf after 24 h		Total no. of nymphs in liquid excrement on all leaves
				Nymphs in spittle (mean $\pm$ SE)	Abandoned spittle masses (mean $\pm$ SE)	
4.4	16	3.33 $\pm$ 0.04	3	4.4 $\pm$ 0.4	1.3 $\pm$ 0.3	1
0.0	16	2.48 $\pm$ 0.05	3	0.0 $\pm$ 0.0	0.4 $\pm$ 0.2	2

TABLE 5. Mortality after 7 days of nymphs on leaves of *X.strumarium* with increasing concentrations of amino acids in the xylem sap

Actual amino acid concentration in xylem sap (mM)	Amino acid concentration in xylem sap (log μ M)	% mortality after 7 days (mean $\pm$ SE)
0.04–0.10	1.6–2.0	88.2 $\pm$ 5.1
0.10–0.32	2.0–2.5	90.7 $\pm$ 9.3
0.32–1.00	2.5–3.0	23.4 $\pm$ 10.2
1.00–5.00	3.0–3.7	11.4 $\pm$ 5.6

ments. The application of the amino acid solution raised the mean amino acid concentration in the xylem sap from 2.48 to 3.33 log μ M. No nymphs were found with spittle after 24 h on any of the control leaves to which no amino acids were applied. The only evidence of feeding on the control leaves were a total of seven abandoned spittle masses and two nymphs found with liquid excrement.

Since only three nymphs were introduced on to each leaf, the results show that on average 1.4 nymphs moved from the control to the experimental leaf.

Relationship between nymphal mortality and the amino acid concentration in the xylem sap

Nymphs were caged on to all the leaves of each *X.strumarium* plant, with three nymphs per cage. Two cages were placed on leaves of a width greater than 4 cm and one cage on leaves of less than 4 cm in width at its widest point. The cages were removed from a plant after 7 days and the number of nymphs dead or alive, and the instar were noted. The total

number of each nymphal instar were as follows: third, 38 (15%); fourth, 80 (32%); fifth, 134 (53%).

Percentage mortality after 7 days was calculated for all the nymphs on each leaf, regardless of instar. High mean mortalities were suffered by nymphs at low amino acid concentrations (<2.5 log μ M), low mean mortalities at high amino acid concentrations (>2.5 log μ M) (Table 5). An effect of amino acid concentration on mortality is to be expected, though not proven by these results, if amino acids are a major nutrient and energy source for xylem feeders.

Relationship between excretory rate and the amino acid concentration in the xylem sap

Table 6 shows the mean excretory rates of nymphs and adults of *P.spumarius* caged individually on to *X.strumarium* leaves with different amino acid concentrations in their xylem sap. Excretory rate increases with increasing amino acid concentration, except in fifth instar nymphs.

The maximum mean rates for nymphs were similar to the mean rates for nymphs on *Pisum sativum* L. in the laboratory. The maximum mean rates for adults were just less than the hourly rates (multiplied by 24) of continuous excretion for adults on *Vicia faba* L. (Horsfield, 1976).

Effect on the excretory rate of adult P.spumarius of amino acid solutions applied to detached X.strumarium leaves

The excretory rate of adults feeding on detached *X.strumarium* leaves increases with

TABLE 6. Excretion by *P.spumarius* on *X.strumarium* leaves with increasing concentration of amino acids in the xylem sap

Stage	Excretory rate (g/24 h) (mean $\pm$ SE) at following amino acid concentrations* in xylem sap (log μ M)		
	<2.5	2.5–3.0	>3.0
Third instar nymph	0.06 $\pm$ 0.02	0.13 $\pm$ 0.02	0.23 $\pm$ 0.02
Fourth instar nymph	0.24 $\pm$ 0.04	0.94 $\pm$ 0.06	0.86 $\pm$ 0.08
Fifth instar nymph	1.14 $\pm$ 0.14	1.35 $\pm$ 0.11	1.21 $\pm$ 0.12
Adult male	0.27 $\pm$ 0.12	0.77 $\pm$ 0.11	1.24 $\pm$ 0.15
Adult female	0.62 $\pm$ 0.16	1.55 $\pm$ 0.18	1.98 $\pm$ 0.22

* There were few values of excretory rates at amino acid concentrations <2.0 and >3.5 (log μ M).

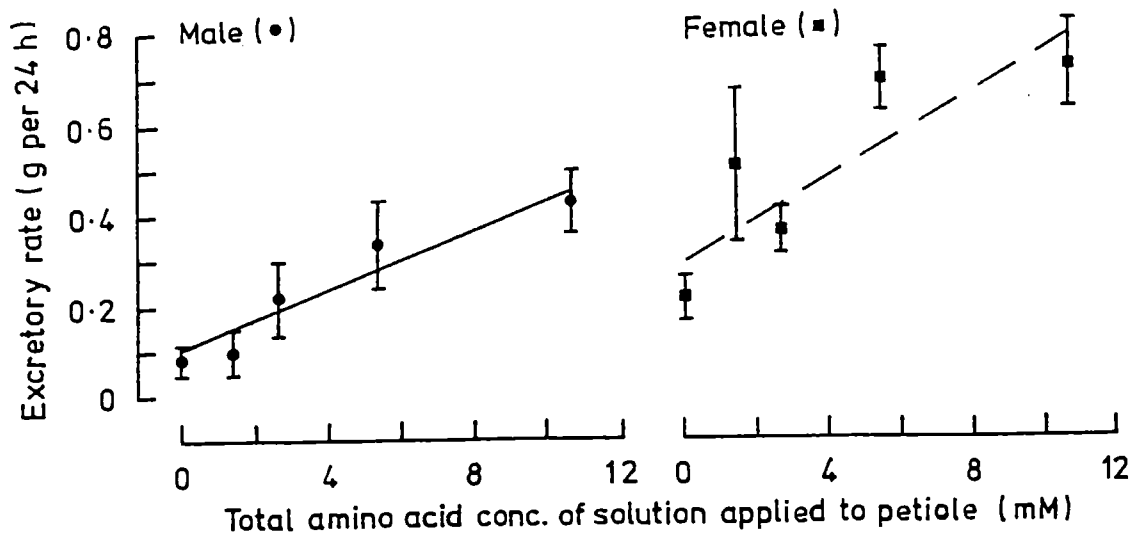


FIG. 3. The relationship between the excretory rate of adult *P. spumarius* (g/24 h) and the amino acid concentration (mM) of solutions supplied via the cut petiole to detached *X. strumarium* leaves. Points are mean excretory rates, bars $\pm$ SE. Regression equations: male, $y = 0.32x + 0.10$; female, $y = 0.047x + 0.29$.

the increase in the amino acid concentration of solutions supplied to the leaf via the cut petiole.

Linear regressions of excretory rate on amino acid concentration (Fig. 3) gave correlation coefficients of $r = 0.53$ ($n = 44$) and 0.42 ($n = 122$) ($P < 0.001$) for male and female respectively. The slopes of the linear regression lines were significantly different from zero ($P < 0.001$).

Discussion

Nymphs of *P. spumarius* selected the younger leaves of *X. strumarium* with relatively high amino acid concentrations in the xylem sap (Table 2, Fig. 2). Selection or rejection of a host leaf for feeding by a nymph depended upon internal factors in the plant (Table 3).

When feeding, nymphs selected detached leaves to which a solution of amino acids was applied in preference to similar leaves to which no amino acids were applied (Table 4). The results do not permit the conclusion that the amino acids *per se* acted as a phagostimulant, since the solution within the xylem vessels is subject to the influence of the surrounding tissues of the leaf. Substances acting synergistically on feeding may have been present in the solution, without which no feeding response would have been elicited.

Similarly, feeding inhibitors may have been removed from the applied solution. Work on artificial diets has established a sugar-amino acid synergism for aphids (Auclair, 1965; Mittler, 1967; Mittler & Dadd, 1964) where the addition of amino acids (singly or as mixtures) strongly enhanced the acceptability of sucrose solutions. The only conclusion permitted by the observations on detached leaves was that a certain concentration of amino acids in the xylem sap (whether acting with a synergist or not) was necessary for the selection of a feeding site by *P. spumarius* nymphs.

Similarly, the increases in mean excretory rate of third and fourth instar nymphs and adult *P. spumarius* (Table 5, Fig. 3) may not be due to the phagostimulatory effects on ingestion of amino acid concentration alone. Synergistic interactions may occur with other substances in the xylem sap or amino acid concentration may be correlated with other factors, responsible for the observed changes in excretory rate.

Studies with artificial diets have shown that amino acids alone did not induce feeding in aphids (Mittler, 1967; Srivastava & Auclair, 1971). However, a synergistic interaction occurs between sucrose and amino acids. Mittler (1970) found a progressive increase in uptake of diet by *Myzus persicae* (Sulzer) associated with an increase in methionine

concentration from zero to 40 mg/100 ml (in the presence of a basal diet containing mineral salts, other nutrients and amino acids, and 15% sucrose). No further increase or decrease in uptake was observed when the methionine concentration was progressively increased to 320 mg/100 ml. Srivastava & Auclair (1974) found that increased concentrations of amino acids up to 3.5% for first to third instar nymphs, and 2.5% for fourth instar nymphs to adults, increased the rate of ingestion of *Acyrtosiphon pisum* (Harris). Ingestion declined from the optimum up to 5% amino acid, the highest concentration used. The effects were tested in the presence of a basal diet with 35% sucrose.

Acknowledgments

I gratefully acknowledge a Natural Environment Research Council studentship and supervision by Dr J. B. Whittaker. Dr T. A. Mansfield provided the pressure bomb.

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Received 28 February 1977

THE BIOLOGY OF *CLASTOPTERA ARBORINA* BALL (HOMOPTERA: CERCOPIDAE) IN WISCONSIN

F. M. KUENZI and H. C. COPPEL
Department of Entomology
University of Wisconsin-Madison

Abstract

Clastoptera arborina Ball is a spittlebug (Homoptera: Cercopidae) that feeds on *Juniperus* and has been recorded recently in Wisconsin. It is univoltine, with the eggs hatching early in June, and the nymphs developing through five instars until early to mid July. Adults appear in early July and persist through early October. Nymphs spend most of their time feeding, primarily on the sap of the green succulent tissue. The fluid waste is formed into a frothy mass (spittle) in which the nymph lives. They usually stay within a few centimeters of their first feeding site while immature. The imaginal molt occurs outside the spittle. The adults are relatively freely living, capable of jumping and flying several meters or more. Adults also spend much time feeding. Mating is done in an end to end configuration and can last up to five hours. Eggs are deposited singly or in pairs under thin flaps of juniper bark. No parasitoids were collected, but the adults may fall prey to a variety of arthropod and vertebrate predators. No physical damage to the host was observed; however, large numbers of nymphs producing the spittle-like froth may be unsightly on ornamental plantings.

INTRODUCTION

Ornamental conifers, including the many varieties of juniper (*Juniperus* spp.) and white cedar (*Thuja*) are widely used in landscape plantings. Their range of color and shape, tolerance of dry conditions, and longevity make them ideal low maintenance plants for beautifying the many harsh environments created by human habitation and business. Insects that damage the aesthetic value of these plants therefore, can become as economically important as those that cause physical and physiological damage. Some species of spittlebugs (Homoptera: Cercopidae) are known to directly damage the host by causing yellowing and browning of the leaf tips, and by vectoring a wide variety of pathogenic organisms (Hamilton, 1983; Wilson and Dorsey, 1957). The spittle bug, *Clastoptera arborina* Ball utilizes *Juniperus* and perhaps *Thuja* as a host. The

nymphal excreta of *C. arborina* is a white, frothy fluid deposited around the insect's body in the form of a spittle-like globule, and many such globules can be unattractive when viewed against the dark green foliage of most varieties. It also feeds on native *J. virginiana* L., which is an important part of the dry, rocky bluff and glade habitats common in Wisconsin. Therefore, both because of its possible economic significance, and because little is known about the general biology of the genus *Clastoptera*, we shall present our observations on the development, behavior, and ecology of *C. arborina*.

SYSTEMATIC POSITION, DISTRIBUTION, AND HOSTS

Clastoptera arborina (Homoptera: Cercopidae) was described by Ball (1927) as *C. obtusa* var. *arborina*, a color variety of what he considered to be a species based on struc-

tural information. The following year Doering (1928), realizing that an even more detailed structural examination was necessary to classify within the genus, published a revision in which the *arborina* variety was given species status. This scheme was maintained in her later keys of the Cercopidae (Doering, 1930, 1941). Hamilton (1978) found that she had misidentified her specimens of *C. arborina* in 1928 as *C. newportae* Doering, a new species, and had described a truly new species as "*C. arborina*." Therefore, he synonymized *C. newportae* with *C. arborina*, and renamed the new species. This revision is maintained in his later key (Hamilton, 1983).

Ball (1927) originally recorded *C. arborina* from Muscatine, Iowa. Doering (1928) recorded collections (as *C. newportae*) from Connecticut, Lakehurst, NJ; Lake George, NY; and Newport, RI. Hamilton (1983) described its distribution from southern Ontario, south to N. Carolina and west to Iowa.

The type specimens were collected from "white cedar," presumably *Thuja occidentalis* L., by Ball (1927). However, Hamilton (1978) was unable to confirm this, but collected many specimens from eastern red cedar, *Juniperus virginiana* L.

INVESTIGATIONAL STUDIES

Ten specimens of the insect collected in 1981 by H.C.C. were identified as *Clastoptera arborina* by J. P. Kramer of the Beltsville Agricultural Research Center, USDA, Beltsville, MD. This series and additional collections from 1983 and 1984 are kept in the research collection of the University of Wisconsin-Madison, Department of Entomology. *C. arborina* was first recorded in Wisconsin from a *J. virginiana* planting in the southwest section of Madison, WI, where this study was subsequently undertaken on populations of *C. arborina* in: a residential area, the Odana Hills Golf Course, and two areas in the University of Wisconsin-Madison Arboretum: the Longe-

necker Horticultural Gardens, and the Juniper Knolls.

MATERIALS AND METHODS

Number of Instars:

Dyar's law, that a dimension of a sclerotized structure should increase by a constant ratio between instars, was used to determine the number of instars of *C. arborina*. Every two days at least 10 spittle masses were collected from the field and taken to the laboratory. The nymphs were removed from the spittle singly and partially dried on ground glass using cross pins for manipulation. The greatest width of the head was measured under a stereo microscope at approximately 54X with a calibrated ocular micrometer. The daily sample size was not constant because some spittle masses contained more than one nymph, and all available nymphs were measured to ensure an adequate number of each instar for further study.

To determine the size of each instar, the measurements were grouped according to instar and numbered consecutively within the group. A random sample of 30 was obtained by using the total data, or a random sample chosen with the aid of a random number table (Snedecor and Cochran, 1980). The data are primarily from 1983, except for the measurements of the first instar, and additions to the second and third instars to complete the sample.

Seasonal History:

Random samples of 20 spittle masses were obtained approximately every other day, beginning with the first sighting of spittle on May 6, 1984. Randomization was done by constructing a grid over the surface of a juniper bush. At every sampling, 20 coordinates were drawn from a random number table (Snedecor and Cochran, 1980), and the spittle mass nearest each coordinate was removed from the bush. From head capsule size or general morphology, all nymphs were

classified according to instar, and the frequency distribution (% of each instar) was recorded for each sampling day. When adults were found, the procedure was modified by counting either the fifth instar exuvia, patches of meconia, or both, if present, as an adult. Actual adult insects were not counted. This interpretation proved unambiguous, as the exuvia and meconia persisted in place for several days.

Hosts:

The plantings of *Juniperus* spp. and *Thuja occidentalis* in the University of Wisconsin-Madison Arboretum provided a unique opportunity for the investigation of hosts of *C. arborina*. Within the Longenecker Horticultural Garden, the "Pinetum" collection contained 32 cultivars of *J. chinensis*, 9 cultivars and varieties of *J. communis*, 1 *J. rigida*, 3 cultivars of *J. sabina*, 1 cultivar of *J. scopulorum*, 1 cultivar of *J. squamata*, and 18 cultivars and varieties of *J. virginiana*. All of these were in a 5600 m² area on a south facing hillside. A neighboring area contained more cultivars of *Juniperus* spp. and a hedge of *T. occidentalis* in juxtaposition. The other area of importance was the Juniper Knolls, which included a large area of juniper canopy and its fringe of isolated and semi-isolated *Juniperus virginiana* trees. A stand of *T. occidentalis* was located 50 m to the east, and the two areas were separated by an extension of the prairie habitat.

When the *C. arborina* nymphs were beginning the fifth instar, all plantings in the above areas were searched extensively for spittle masses. Approximately one month after the appearance of adults, a second survey was conducted including these same areas and the plantings around the administration building. In this study, adults were collected by sweeping the foliage with an insect net.

To determine the part of the plant utilized, the spittle masses observed in the seasonal history survey were scored according to the part of the branch they occupied. The cate-

TABLE 1. Head capsule measurements for nymph and adult stages. n, sample size; $\bar{x} \pm SD$, mean $\pm$ standard deviation; Ratio, nymphal instar/previous instar

Instar	n	$\bar{x} \pm SD$	Range	Ratio
I	30	0.333 $\pm$ 0.011	0.32 - 0.36	
II	28	0.485 $\pm$ 0.021	0.45 - 0.52	1.4:
III	30	0.695 $\pm$ 0.037	0.60 - 0.76	1.4:
IV	30	1.038 $\pm$ 0.047	0.90 - 1.13	1.4:
V	30	1.552 $\pm$ 0.080	1.35 - 1.70	1.5:
Adult	30	1.841 $\pm$ 0.080	1.66 - 1.96	
male	15	1.809 $\pm$ 0.080	1.66 - 1.94	
female	15	1.872 $\pm$ 0.068	1.72 - 1.96	

gories were: a) "Core," including the trunk, major branches, and minor branches covered with true, cambium-derived bark; b) "Dry Twig," or the smaller branch covered with dried scales; c) "Green Twig," or the photosynthetic twig composed of long scales, concurrent proximally with only the tip free; and d) "Foliage," which in most varieties takes the form of branchlets bearing small, closely appressed scales.

RESULTS AND DISCUSSION

Number of Instars:

Head capsule measurements clearly differentiate five nymphal instars (Table 1). The growth ratios are reasonably constant and generally agree with the 1.4 expected from Dyar's law. The ranges of the 5th instar and the adult measurements overlap but the head capsule width is otherwise diagnostic for each instar. The adult and nymph are easily distinguished morphologically. There is a significant difference ($P < 0.05$) between the adult male and female measurements, and the increasing standard deviation with each instar (Table 1), particularly in the case of the 5th instar, may be partially due to this sexual dimorphism. Unfortunately, a lack of preserved specimens prevented statistical testing of the immatures.

Descriptions of Stages and Instars:

Egg (fig. 1): The egg is elongate, oval, and 0.835 ± 0.057 mm ($n = 16$) long. In the fall

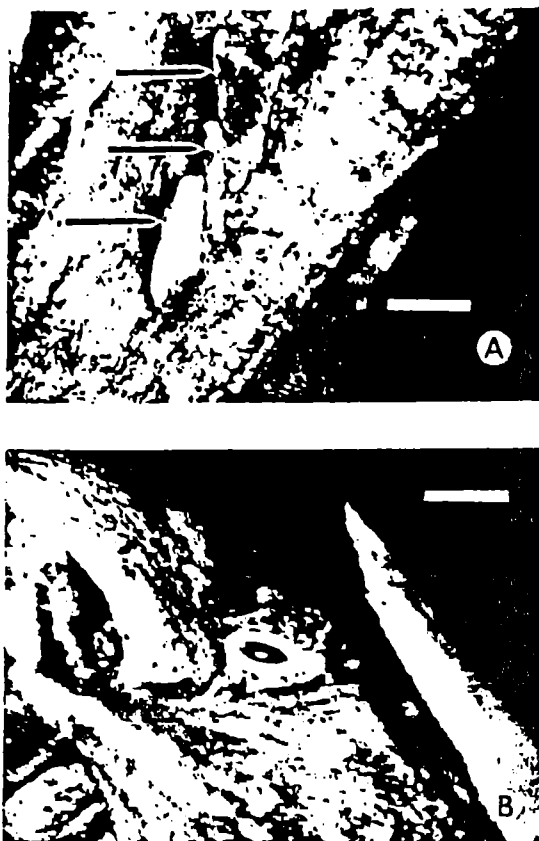


Fig. 1. *Clastoptera arborina* eggs in situ: A) during the fall (3 eggs, side view), and B) in the spring before hatching (1 egg, face view). Note the shiny black "egg burster" in B. Bar equals 0.5 mm.

laterally flattened, with the broad side 362 ± 0.061 mm ($n=15$) wide, and the narrow side 0.197 ± 0.037 mm ($n=12$). It is deposited under a flap of the plant tissue with one end and most of a side ($\frac{1}{4}$ to $\frac{1}{2}$ of the circumference) remaining exposed. The exposed end is more pointed and narrower than the blunt inner end. A white patch of thickened chorion covers the central portion of the exposed area, but the peripheral chorion, like that covered by the bark or epidermis, is membranous and translucent to the yellow yolk. The white patch has a dark sagittal streak under the chorion. In the spring the egg swells, becoming round and splitting the chorion over the streak to expose a shiny black, oval "egg burster" (fig. B).

First Instar (fig. 2A,B): The head is

yellow, round, and the width at the eyes is little more than the clypeus. The labium is surprisingly long compared to the total body length, and in dorsal view protrudes beyond the tip of the abdomen. Each eye consists of ten pigmented ommatidia. The antennae are short and two-segmented.

The thorax is yellow, cylindrical, narrower than the head, and dominated by the pronotum. The mesonotum has lateral triangular sclerotizations, and the metanotum is entirely membranous. The legs are translucent, long, and spider-like. The tarsi are two segmented.

The abdomen is initially yellow, contracted, only slightly wider than the thorax, and carried with the tip directed dorsally. After feeding it becomes distended (fig. 2B). There is a shallow groove parasagittally which marks the attachment of the dorso-ventral muscles, and there are irregular transparencies in the integument permitting partial observation of the digestive and circulatory organs. Paired, brush-like structures of transparent filaments occur ventrally on segments 5 and 6 (fig. 3). These are shed with the exoskeleton at each molt. Similar structures are on segments 7 and 8 of *L. quadrangularis* and *Aphorophora parallela* Say (Guilbeau, 1914). Unlike the condition in *Tomaspis saccharina* Dist. (Kershaw, 1914), *Lepyronia quadrangularis* (Say) (Doering, 1922), and *Philaenus lineatus* (Sulc, 1910), the terga actually fuse in the ventral midline rather than merely touch or overlap (fig. 2G). The last tergum (9) is sclerotized, and its lateral edges curve ventrally and touch without fusing. Thus, the air canal enclosed by the sterna is a complete tube, closed anteriorly by a posteriorly directed triangular ridge of sternum 3, and open posteriorly at the margins of tergum 9. The remainder of the abdominal cuticle is unsclerotized.

Second Instar (fig. 2C): The second instar resembles the first, although it is larger. The eyes consist of 12-15 ommatidia on a widening of the head, and the antennae are short

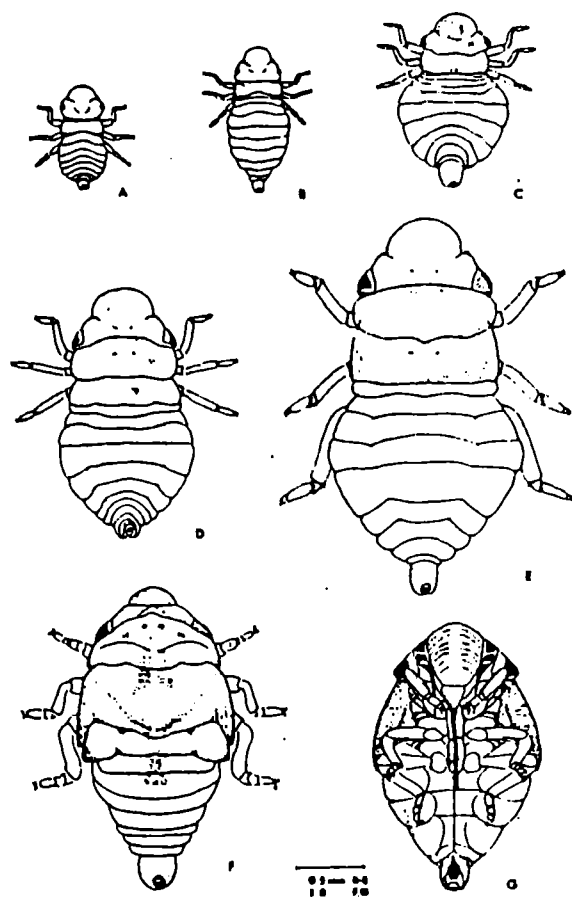


Fig. 2. Nymphal instars of *C. arborina*. A) newly emerged nymph; B) late first instar; C) second instar; D) third instar; E) fourth instar; F) fifth instar, dorsal view; G) fifth instar ventral view. Note the different scale for F and G.

and two-segmented. The thorax is more dorsoventrally flattened, and dominated by the prothorax. There is some sclerotization of the lateral meso- and metanota. The head, thorax and last abdominal tergum are usually olive green, and the remainder of the abdomen is yellow.

Third Instar (fig. 2D; 3A): The head is olive green and broad. The eyes are hemiconical and multifaceted, with the distal ommatidia darkly pigmented. Each antenna has two basal and one flagellar segment, and the ocelli first appear.

The thorax is dorsoventrally flattened, with the pro- and mesonota prominent. The

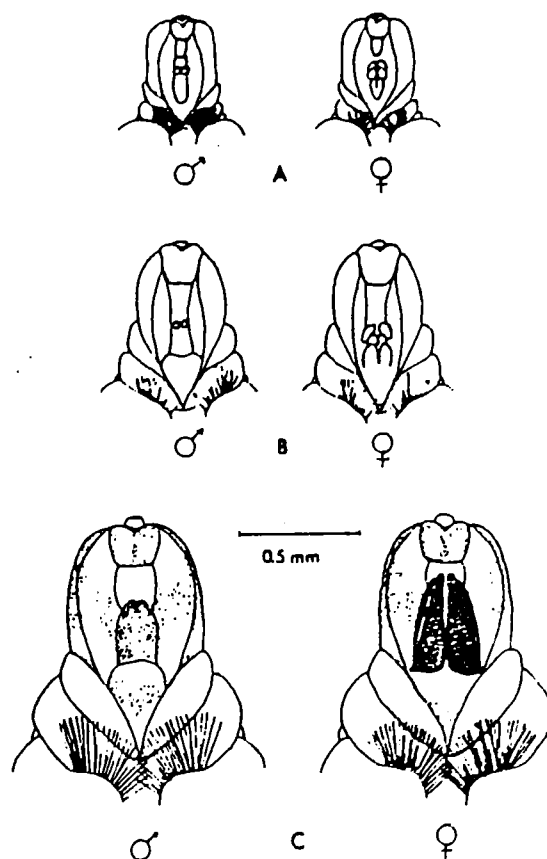


Fig. 3. Development of the genitalia. Ventral views of abdominal segments 5-9. Segment 6 is concealed by the enlarged fifth tergum and the curvature of the aldomen. The filaments mentioned in the text are shown as one clump. A) third instar; B) fourth instar; C) fifth instar.

legs and dorsal thorax are olive green. Wing pads become evident in this instar.

The abdomen is light yellow, although some internal organs may impart a greenish tinge. The ventrolateral areas of segments 4 and 5 may appear bright orange, due to a number of large pigmented cells in the body cavity of this region. Similar tissue was reported by Garman (1923) as the "spittle gland" of *C. obtusa* Say, and is also found in *L. quadrangularis* (Doering, 1922). The developing male and female genitalia become evident in the ninth sternal region (fig. 3A).

Fourth Instar (fig. 2E; 3B): The fourth instar is generally similar in form and color to

the third instar. The antennae have two basal segments, but flagella have a number of irregular, colored bands suggestive of segments. The sclerotized structures are olive green, although the shade is highly variable, and the head and thorax have dark patches. Anterior wing pads are prominent, and trachea can be seen entering them. Posterior wing pads are slightly developed. Each leg bears a fringe of apical tibial spurs.

Fifth Instar (fig. 2F,G;3C): Dorsally the head is crescent-shaped due to further broadening and shielding posteriorly by the pronotum. The color is olive green. Antennae are long and filamentous.

The thorax varies from dark green to grey or brown, and the darkening of the midline and wing areas makes it appear three-striped. The anterior wing pads are well developed, and exhibit some of the features of the adult tegmina. The posterior wing pads are less well developed and appear as lateral triangular thickenings. The meso- and metathoracic legs each bear a comb of apical spines, and all tarsi are three-segmented. Late in the stadium, black-tipped adult tibial spurs are visible under the nymphal cuticle.

The first abdominal segment is sclerotized and colored like the thorax. The second segment has a triangular, darkly pigmented patch, anteriorly as wide as the margin in dorsal view and narrowing to a point halfway along the midline. The remainder of the abdomen, except for the last tergum can be yellow or white depending on the individual. The genitalia are plainly visible on the last sternum; the valves of the ovipositor are jet black, and the claspers of the male are dark and sclerotized (fig. 3C).

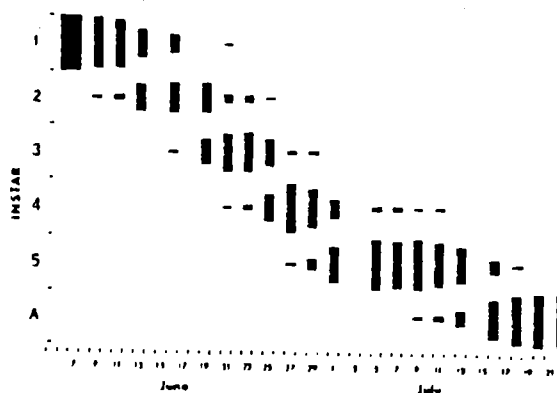
Adult: Doering (1928) illustrated and described the adult in detail as *C. newporta*. We have found that the ovipositor's third valvulae are fused dorsally for one third their length and bear 68 ± 5.57 ($n = 25$) teeth along the dorsal margin between the fusion and the apex. Doering (1928) reported "about 82 teeth" for *C. arborina* while *C. doeringae* Hamilton has "81 to 90" and *C.*

media Doering has "about 78." The structure of these valvulae is supposed to be of great comparative value for these closely related species. The red abdominal tissue is well developed, but not visible due to the pigmentation of the integument.

Seasonal History:

Clastoptera arborina is univoltine in Wisconsin, and overwinters in the egg stage. This is consistent with most other *Clastoptera* at this latitude on the continent, e.g. *C. hyperici* Gib. in Michigan (Hanna, 1969), but differs from the bivoltine *C. obtusa* of Connecticut (Garman, 1923).

The seasonal distribution of the different instars from the 1984 data (fig. 4) generally corresponds to the 1983 observations. Eggs with the "egg burster" were found in the third week of April, 1984. First instar nymphs were found on June 6, 1984, and an egg was observed hatching June 7, 1984. In both 1983 and 1984, adults began to appear in early July. Mating was first observed in mid July, and observations of mating continued into early October, when the last adults were collected (both years). Eggs were found in twigs caged with adults from July 27 to September 26, 1984. The seasonality of *C. hyperici* is similar to this, although Hanna (1969) does not give specific dates, and Garman's (1923) records for the species



mentioned above show a slightly contracted seasonality, with the first generation being advanced about 3 weeks.

Hosts:

Nymphs and/or adults of *C. arborina* were found on the following cultivars or varieties of *Juniperus* spp: *Juniperus chinensis* cultivars Ames, Blaauw, Columnaris Glauca, Fairview, Iowa, Keteleeri, Mission Spire, Mountbatten, Obelisk, Pfitzerana Aurea, Pfitzerana Glauca, Robusta Green, and Story; *Juniperus communis* cultivar Laxa; *Juniperus sabina* cultivars Fastigata and Von Ehren; and *Juniperus virginiana* from Juniper Knolls and cultivars Burkii, Canaertii, Globosa, Hillii, Hillspire, Pyramidalis, Skyrocket and variety glauca. A large collection of *J. horizontalis* was not examined for spittle masses, and no adults were collected; however, the low creeping growth of this species made the sweeping technique ineffective. *J. rigida*, *J. squamata*, and *J. scopulorum* supported neither nymphs nor adults, but together they made a small contribution to the total planted collection. Otherwise *C. arborina* is able to complete development on several species and varieties of *Juniperus*. Doering (1942) listed three other *Clastoptera* spp. collected from *Juniperus*, including *C. elongata* Doer., *C. juniperina* Ball, and *C. doeringae*.

Both the nymphs and adults of *C. arborina* prefer to feed on the green twigs of *Juniperus*. A Chi square (χ^2) test against the null hypothesis of equal utilization of the four areas was highly significant (Table II, $P < 0.05$). The green twig was the preferred

feeding site, as this category made the greatest contribution to χ^2 . Also only 5th instar nymphs and adults were found in the dry twig area, which can be attributed to the relocation of spittle masses toward the trunk as described below, and the free movement of the adults respectively.

Habits of the Nymphs:

Eclosion: The "egg burster" acts as a trap door at hatching, as its seam breaks cleanly through most of its circumference. The nymph is positioned in the egg with its head in the outer tip and its venter against the "egg burster." As it wriggles out of the chorion, its legs are worked free, and extended and flexed repeatedly until one catches an object such as a scale or twig. This action enables the nymph to pull itself into a standing position. The time from chorion rupture to complete eclosion is approximately 5-10 min. The nymph remains nearly motionless for about 20 min, after which it begins crawling about the foliage and twigs until it establishes the first feeding site.

Spittle Production: Doering (1922) briefly reviewed earlier accounts of bubble forming movements and related morphology in cercopid nymphs. In general, her description and conclusions accurately apply to the observations of *C. arborina* nymphs. As noted previously, four clusters of filaments are present near the opening of the air canal. Guilbeau (1914) reported that they are a secretion of the dermal glands of Batelli. His experimental and histological studies indicated that the secretion is necessary for the retention of bubbles in the excrement. We observed that the filaments usually come in contact with the newly formed bubbles as they are expressed from the air canal, so they may indeed contribute to this phenomenon.

Spittle production and maintenance was virtually continuous; however, the rhythmic movements of bubble making were frequently interrupted by short, ca 30 sec periods of breathing, where only a small "Y"-shaped

TABLE 2: Parts of the juniper plant utilized for feeding by *Clastoptera arborina*.

Stage	Dry		Green	Foliage	Total	χ^2 *
	Core	twig	twig			
Nymph	0	7	124	40	171	227.24
Adult	0	19	44	16	79	50.27

* 3 degrees of freedom.

vent (the space on either side of the anus and the adjoining median cleft between the tergal plates) was open for the passage of air into the air canal.

Activity: Nymphs are generally sedentary, although they are capable of rapid movement while immersed in the spittle. The principal activity is feeding, with the stylets inserted in the plant tissue. This necessarily renders the insect immobile, except for the abdomen, which is almost continually pumping back and forth. When the spittle is disturbed however, the nymph will withdraw its abdomen from the surface and its mouthparts from the plant, move to the opposite side of the twig, and take shelter in the axil of a scale if available. Usually the mass of froth is sufficient to obscure the presence and movements of a completely submerged nymph. The insect may remain submerged for at least a minute, although, unless disturbed again, it will protrude its abdomen

and begin bubble making within a few seconds. Molting from one nymphal instar to another takes place inside the spittle mass, and one to several exuvia can be found floating in the fluid after the first instar.

A nymph may abandon its original spittle mass and move to a new feeding site, usually on the same branch. Most abandoned spittle masses are a result of this relocation rather than nymphal death. This is based on observations of the number and location of spittle masses on marked twigs. The new masses were usually closer to the center of the plant. The number of exuvia in fifth instar spittle also suggests that this movement occurs during the third or fourth stadium. Wandering nymphs carry a film of spittle over their backs, and a cache of bubbles and fluid around their coxae. They crawl randomly, and intermittently probe the twig surface with their labellum until a new feeding site is found. If they contact another spittle mass however, they stop and enter it. This sometimes leads to aggregations of up to 8 nymphs in one continuous spittle mass (fig. 5). This is no doubt a common feature of the immature *Cercopidae* (Hamilton, 1983).

Natural Enemies: Nymphs may fall prey to a variety of arthropod predators, primarily of the order Hemiptera (Insecta) (Hamilton, 1983). Although we found no direct evidence of this, members of the family Reduviidae, Nabidae, Pentatomidae, and Miridae were found on juniper in association with *C. arborina*. One case of an ectoparasitic larva was observed, but it died soon after discovery, and no identification was made. It did bear resemblance to the illustrations of the drosophilid found on temperate *C. obtusa* (Baerg, 1920; Garman, 1923).

Impact: In spite of sometimes heavy feeding, we observed neither yellowing nor browning of the branchlet tips nor significant necrosis of the tissue around feeding sites. Thus, the physical or physiological damage caused by *C. arborina* is likely to be minimal for plants in unstressed environments.



Fig. 5. Aggregation of eight fifth instar nymphs.

Habits of Adults:

Imaginal Molt: The final molt occurs outside and usually towards the tip of the branch from the last spittle mass. Newly emerged adults are pale yellow without definite markings. As the thorax is freed from the nymphal skin, the wings are expanded, while being held in a vertical position. The legs and abdomen are then pulled free, and the genitalia are expanded to full size, and spread. After complete expansion, the wings are first lowered till horizontal and longitudinal to the body axis, and then slowly, ca 2 min, laid flat on the back. Emergence takes approximately 20 min. Failure to molt properly is a frequently observed mortality factor.

After molting, the adult may crawl a short distance before pausing for cuticular tanning. Development of the mottled white, tan, and black markings usually requires two or more hours, during which time the meconium is cast. The meconium is splattered on the foliage, and dries as a white plaster-like substance, resistant to rain, and persisting through the fall. After feeding, adult excreta is also splattered on the foliage as droplets of transparent fluid.

Locomotion: The adult *C. arborina* is essentially sedentary, spending much time feeding and mating, and it will usually tolerate the manipulation of foliage necessary for close observation. Short distance movement is by crawling, with the anterior four legs used in the typical insect gait, and the metathoracic (jumping) legs either held next to the abdomen in a "cocked" position, or used in an anterior-posterior pushing motion. Jumping is accomplished by an explosive extension of the hind legs, accompanied by a slightly audible popping noise. About 15 sec is required for cocking the legs after landing. Jumping is a frequent means of escape, but has also been observed in the froghopper's unmolested activity. In addition, after jumping, *C. arborina* may use its wings to alter its course, or extend its range several meters. Specimens of *Clastoptera*

spp. were captured in the 20 m tower at Bell Plain, NJ (New Jersey Dept. Agr., 1927) which indicates a potential for long range dispersal of these insects, probably mediated by active flying.

Mating: During courtship the male rides on the back of the female, with the couple facing forward. The male and female genitalia are then coupled and mating begins. The pair may continue in this configuration, but usually the male lets loose and turns to face in the opposite direction. While joined, they do not feed, but can crawl in a push-pull fashion, and jump approximately 30 cm vertically. Copulation lasts from two to five hours.

Oviposition: Eggs are laid singly or in rows of 2 or 3 under a flap of either bark (most common, fig. 1), or the green twig or foliage epidermis. When in the latter succulent tissue, a brown necrotic area forms around the egg. The long axis is usually at a 20° to 50° angle with the long axis of the twig, or when laid in the axis of a branch and twig, its direction is nearly perpendicular to the plane of the branch and twig. The egg penetrates the bark and parenchyma, and often the phloem and outer xylem as well. In nature a twig rarely contains more than two oviposition sites.

Fecundity: Ten females dissected between July 25 and August 20, 1984 contained from 6 to 11 ovarioles in each ovary (median = 8). Mature oocytes (length = 0.773 ± 0.053 mm, $n = 28$ from 4 females) were present in the ovarioles and lateral oviducts beginning July 25, but some specimens contained only developing oocytes. From late July to early October all specimens contained one or more mature oocytes, and mating was observed throughout the interval. Unfortunately, adults did not survive more than a week when caged on juniper, so no estimate of total fecundity was possible.

Predation: Adults are probably more susceptible to predation than nymphs, although the small size and cryptic coloration of the former when viewed against the

dry twig may provide some protection. In the laboratory they have been preyed upon by a toad, and a variety of arthropod predators including *Zelus socius* Uhler (Hemiptera: Reduviidae), *Phymata pennsylvanica* Handlirsch (Hemiptera: Phymatidae) and *Misumenops asperatus* (Hentz) (Arachnida: Araneae: Thomisidae), all collected from juniper. The froghoppers were captured by the predators only while moving about between feeding periods, presumably because their motion increased their visibility. Also they could frequently escape even after capture by using their explosive jump.

ACKNOWLEDGEMENTS

This research was supported by the College of Agricultural and Life Sciences, University of Wisconsin-Madison, and by research funds from The Wisconsin Department of Natural Resources through the School of Natural Resources, University of Wisconsin-Madison. We wish to express our sincere gratitude to John Haanstad for the photographic assistance, to Steven Krauth for the taxonomic assistance, to Dr. E. Hasselkus for maps and planting records of the Arboretum collection, and to the staff at the Arboretum for their cooperation.

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Cría masiva de especies de cercópidos en invernadero

S. L. Lapointe, G. Sotelo, M. S. Serrano y G. Arango*

Introducción

La sección de Entomología del Programa de Pastos Tropicales del CIAT trabaja en la búsqueda de especies forrajeras con resistencia varietal a cercópidos, principalmente de los géneros *Zulia* y *Aeneolamia* (Homoptera: Cercopidae), insectos capaces de causar la pérdida total de pasturas de *Brachiaria* y *Panicum maximum*. En el campo las evaluaciones de germoplasma se dificultan por la estacionalidad y falta de uniformidad en los ataques del insecto, lo cual no permite tener infestaciones uniformes para seleccionar plantas con niveles aceptables de resistencia. Además, las poblaciones de cercópidos (conocidos como salivazo, salivero, salivita, mión de los pastos, candelilla, baba de culebra, mosca pinta, y cigarrinha) varían en tamaño de un año a otro, complicando aún más la selección de plantas resistentes.

Hagley (1967) desarrolló una dieta artificial, químicamente definida para criar adultos de *Aeneolamia varia saccharina* (Distant), mejor que su método tradicional de cría sobre hojas de caña de azúcar. Fewkes y Demidecki-Demidowicz (1971) lograron criar *A. varia saccharina* y *A. posticata jugata* (Fowler) durante

algunas generaciones en una cámara diseñada para cría de ninfas, colocando los adultos obtenidos en otra jaula con maíz o caña de azúcar y papel filtro como sustrato de oviposición. Posteriormente se desarrolló una técnica para la cría de *Prosapia bicincta* (Say) sobre *Pennisetum typhoides* (Burm), en cámaras de oviposición que permiten obtener hasta 5600 huevos en un período de 12 días (McWilliams y Cook, 1975); sin embargo, estas técnicas dependen de la presencia de adultos en el campo para mantener un nivel adecuado de población en la colonia. De lo anterior se desprende la necesidad de desarrollar un método que permita la producción continua durante el año de insectos en todos los estados de desarrollo, tal como lo proponen Lapointe et al. (1989).

En esta nota se describe una técnica sencilla y eficiente para la cría masiva en invernadero de *Aeneolamia reducta* y *Zulia colombiana*, las principales plagas de *Brachiaria* en Colombia. Con ella es posible la evaluación de germoplasma en condiciones de invernadero durante todo el año.

Materiales y métodos

Obtención de posturas. Los adultos se confinan en cámaras de oviposición, consistentes en jaulas de madera de 40x40x80 cm con piso removible para introducir una capa de barro colado de 0.5 cm de espesor como sustrato de

* Entomólogos del Programa de Pastos Tropicales del Centro Internacional de Agricultura Tropical (CIAT), Apartado aéreo 6713, Cali, Colombia.

oviposición, y aberturas laterales para el suministro de la alimentación con base en hojas de gramíneas, previamente sembradas en macetas (Figura 1). Los insectos permanecen en estas condiciones durante una semana, al final de la cual se retiran el sustrato de oviposición y los adultos muertos.

En el sustrato de oviposición se hacen cortes en forma reticular para proporcionar sitios de postura; las hembras utilizan los bordes de las ranuras para sujetarse y ovipositar. La extracción de los huevos del sustrato se hace semanalmente mediante el lavado y cernido en tamices. Los huevos se separan por flotación en solución salina al 30%; se desinfectan con hipoclorito de Na al 2% durante cinco minutos y se incuban a temperatura ambiente en platos petri en papel filtro con humedad de saturación. Cuando están próximos a eclosionar, es decir; cuando presentan la sutura de eclosión y manchas rojas bien definidas en cada extremo (Figura 2), se colocan en grupos sobre papel filtro húmedo y se trasladan a las unidades de cría de ninfas.

Los huevos se clasifican por su estado de desarrollo, aprovechando las diferencias en

densidad específica a medida que avanza el proceso embrionario. Para el efecto, se utilizan cuatro embudos de separación, cada uno con una alcuota de las soluciones: 13%, 16%, 19% y 22% de NaCl. Los huevos más desarrollados flotan en la solución al 13% y los menos desarrollados lo hacen en las de 19% y 22%. Mediante la separación de cada uno de los grupos flotantes se mantienen reservas de huevos, clasificados en diferentes estados de desarrollo embrionario. Los huevos infértiles o dañados se precipitan en la solución al 22% de NaCl (Figura 3).

Cría de ninfas. Las ninfas se crían sobre raíces de *Brachiaria ruziziensis* CIAT 654, las cuales no se deterioran, soportan la población y permiten un buen desarrollo ninfal. La siembra de la gramínea se hace de tal forma que permita el

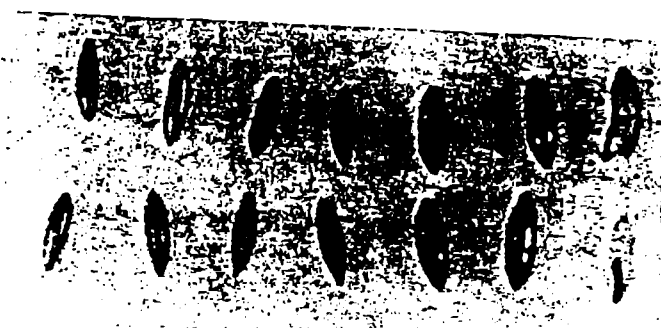


Figura 2. Vista lateral (arriba) y dorsal (abajo) de huevos de *Zulia colombiana* en varias etapas de desarrollo embrionario. A la izquierda, huevos recién colocados y al extremo derecho, coriones vacíos.

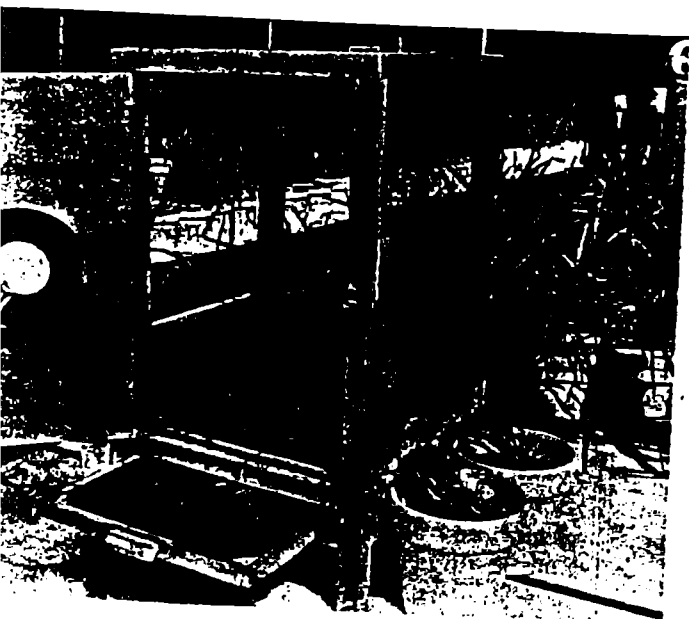


Figura 1. Cámara de oviposición con piso removible y sustrato de oviposición (barro colado).

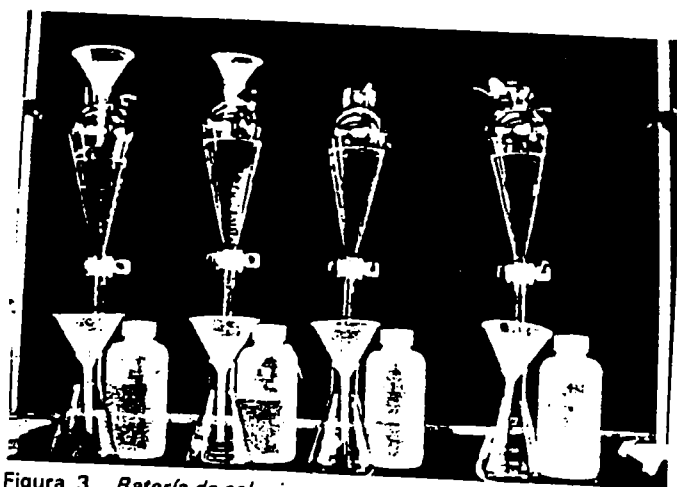


Figura 3. Batería de soluciones salinas a diferentes concentraciones para separación de huevos en sus diferentes estados de desarrollo embrionario por flotación.

desarrollo de raicillas secundarias expuestas superficialmente; esto se logra mediante el enraizamiento en recipientes de cartón (Jiffy-pots) del material vegetativo recolectado en el campo. Después de 3 semanas las plántulas se transplantan a macetas plásticas de 20.5 cm de diámetro que contienen suelo hasta 3/4 de su capacidad. Para el trasplante se rompe el recipiente 'Jiffy' y la plántula se traslada a la maceta plástica, en la cual previamente se coloca una lámina de plástico o de metal de 15 cm de diámetro como barrera para impedir el crecimiento vertical y favorecer el crecimiento lateral y superficial de las raíces.

Para mantener una alta humedad relativa en la maceta, ésta se cubre con una tapa de aluminio pintada de blanco (Figura 4), con lo cual se logra mantener porcentajes de humedad como los que aparecen en la Figura 5. La oscuridad que proporciona esta tapa estimula el crecimiento de raicillas secundarias laterales que son los sitios



Figura 4. Planta de *B. ruzienseis* sembrada en maceta plástica de 20.5 cm de diámetro con una tapa de aluminio pintada de blanco. Nótese las espumas de las ninfas.

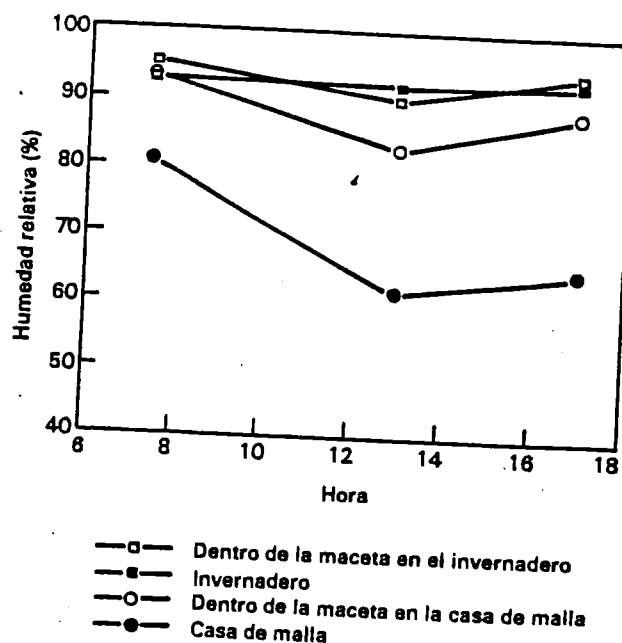


Figura 5. Humedad relativa en la casa de malla en el invernadero y en la unidad de cría de ninfas de *Aeneolamia reducta* (bajo tapa de aluminio).

preferidos de alimentación de las ninfas. Cuando las plantas tienen 3 semanas de transplantadas presentan un buen desarrollo radicular, época en la cual se infesta cada una con 30 huevos próximos a eclosionar y se mantienen en la 'casa de malla' durante todo el tiempo de desarrollo de las ninfas. El piso de la casa de malla se debe regar con frecuencia para evitar altas temperaturas.

Obtención de adultos. Veinticinco días después de la infestación, cuando las ninfas están próximas a mudar al estado adulto, las macetas se trasladan a las cámaras de captura. La captura se hace mediante la remoción de las tapas de aluminio y recolección de los especímenes, aprovechando el hábito del insecto adulto de permanecer dentro de la espuma ninfal durante algunas horas. Esto permite sexarlos individualmente y trasladarlos a las cámaras de oviposición para continuar el ciclo de la colonia. Los adultos así obtenidos pueden utilizarse en experimentos que requieren el control de la edad o el sexo de los insectos.

Resultados y discusión

Producción de adultos en la colonia. Cuando la infestación semanal de la colonia se hizo con 30 huevos/maceta (150 macetas/ciclo), se

obtuvieron un promedio de 250 ± 135 adultos/día. Actualmente la colonia de *A. reducta* produce, en promedio, $13,800 \pm 6500$ huevos semanales, los cuales se utilizan para evaluar la resistencia genética de las gramíneas a los cercópidos, para estudios de mecanismos de resistencia y de ecología de la plaga y para reinfestación de la colonia. Para evitar la pérdida de agresividad del material producido y mantener la calidad en las evaluaciones, una vez por año se deben añadir adultos recolectados en el campo (Chambers, 1977).

Problemas en el manejo de la colonia. Ocasionalmente se presenta contaminación de las plantas hospederas por áfidos, los cuales encuentran en la casa de malla condiciones adecuadas para su crecimiento y pueden disminuir la cantidad de cercópidos producidos. Sin embargo, la revisión periódica de las plantas y el control manual han sido suficientes para mantener las poblaciones de áfidos a niveles que no causen problemas.

Cuando se introducen insectos o plantas del campo directamente a la colonia, con frecuencia aparecen ataques de *Metarhizium anisopliae*, un patógeno de varias especies de cercópidos. Por lo tanto, durante el establecimiento de la colonia y cada año en los periodos de renovación de adultos es recomendable desinfectar el material de siembra y hacer cuarentena a los adultos recolectados en el campo.

En ocasiones varias especies de hormigas, frecuentes en los invernaderos, pueden causar problemas debido a que se llevan los huevos de las unidades de cría. Para evitar esto se deben aislar las mesas, colocando platos con agua en los sitios de apoyo y separándolas de las paredes.

Conclusión

Esta técnica de cría puede usarse para multiplicar con fines de investigación varias especies de cercópidos, plaga importante de los pastos tropicales. Es eficiente y permite un suministro continuo de insectos, en cualquiera

de sus estados de desarrollo, lo cual facilita la realización de experimentos controlados en forma precisa.

Summary

A simple technique for producing spittlebug nymphs and adults [*Zulia colombiana* (Lallemand), *Aeneolamia reducta* (Lallemand), and others] and a highly efficient method for recovering spittlebug eggs are described. Eggs are recovered from a soil substrate placed in the bottom of an oviposition chamber. Eggs are incubated in petri dishes and separated according to stage of embryonic development by flotation in salt solutions of varying concentrations. Favorable conditions for rearing nymphs are obtained by growing susceptible grass plants in plastic pots with an aluminum cover. The cover maintains high relative humidity inside the pots during nymphal development when ambient humidity is low. Darkness and humidity afforded by the cover also stimulate proliferation of superficial rootlets, thereby providing abundant feeding sites for early instar nymphs. Adults are collected from screen cages. Some problems commonly encountered and their solutions are discussed.

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Antibiosis to Spittlebugs (Homoptera: Cercopidae) in Accessions of *Brachiaria* spp.

S. L. LAPOINTE, M. S. SERRANO, G. L. ARANGO, G. SOTELO, AND F. CORDOBA

Centro Internacional de Agricultura Tropical, A. A. 6713, Cali, Colombia

J. Econ. Entomol. 85(4): 1485-1490 (1992)

ABSTRACT High levels of antibiotic resistance to the cercopid *Aeneolamia varia* (F.) were identified in accessions of the forage grass *Brachiaria* by means of a glasshouse bioassay. Emergence of adults from pots of *Brachiaria* spp. infested with eggs of *A. varia* ranged from 55 to 83% and 56 to 80% on susceptible *B. decumbens* Stapf cv. Basilisk and *B. dictyoneura* (Fig. & De Not.) Stapf cv. Llanero, respectively, compared with 3-33% on the resistant *B. brizantha* (A. Rich.) Stapf cv. Marandu. Eleven accessions from six species of *Brachiaria* were identified as being at least as resistant as 'Marandu' based on adult emergence. Two accessions of *B. jubata* (Fig. & De Not.) Stapf (CIAT 16531 and CIAT 16203) were highly antibiotic. When reared on *B. jubata* CIAT 16531, nymphs that survived until the fourth or fifth instar subsequently died during molt after apolysis was initiated but before ecdysis could be completed, and were malformed. All nymphs that died during final molt were in the pharate condition before ecdysis began or were unable to complete ecdysis. Survival of nymphs beyond the third instar on *B. jubata* CIAT 16203 was very low. When late instars were transferred from 'Basilisk' to *B. jubata* CIAT 16203, survival was reduced compared with nymphs transferred to 'Llanero', and deformations and molt disruption were observed. Molt disruption is postulated to be the mechanism of resistance in *B. jubata* CIAT 16531 and 16203. Adult females produced less excreta when caged on the resistant accessions *B. jubata* CIAT 16531 and 'Marandu' compared with the susceptible 'Basilisk' and 'Llanero'.

KEY WORDS Insecta, Cercopidae, antibiosis, *Brachiaria*

THERE ARE MORE THAN 150 million ha of well-drained savannas in Brazil, Colombia, and Venezuela on which intensified grazing and crop-pasture systems could be implemented. Grasses of the genus *Brachiaria* Griseb. are of increasing importance in these areas because of their excellent adaptation to soils of low pH and resistance to drought. *B. decumbens* Stapf, and *B. humidicola* (Rendle) Schweick have been widely adopted throughout Central and South America and are a key element of the Centro Internacional de Agricultura Tropical (CIAT) objective to provide sustainable, productive, and drought-resistant forage for beef and milk production on acid, infertile lowlands of tropical America. In addition, recent data show that *B. decumbens* can significantly increase soil fertility and crop yield in rotations and relays (Zeigler & Toledo 1992) and could be used to control erosion on Andean hillsides in associations with traditional crops such as cassava.

Productivity and stability of *B. decumbens* and *B. humidicola* pastures are limited throughout Latin America by susceptibility to a complex of native species of spittlebugs comprising eight genera: *Aeneolamia*, *Zulia*, *Delassor*, *Deois*, *Mahanarva*, *Sphenorhina*, *Tomaspis*, and *Prospia*. In spite of its susceptibility to spittlebug damage, *B. decumbens* cv. Basilisk continues to

be the most widely planted *Brachiaria* cultivar because of its excellent agronomic characteristics and adaptation to low-fertility soils. *B. brizantha* (A. Rich.) Stapf cv. Marandu was released in Brazil in 1984 (Nunes et al. 1984). Although 'Marandu' has excellent resistance to spittlebugs (Nilakhe 1987, Ferrufino & Lapointe 1989), it is more demanding in terms of soil fertility than 'Basilisk' and has been adopted only in more fertile areas. More recently, *B. dictyoneura* (Fig. & De Not.) Stapf cv. Llanero was released in Colombia because it is tolerant to spittlebug damage and compatible with forage legumes (ICA 1987). Subsequent studies have shown, however, that 'Llanero' is an excellent host for spittlebug nymphs (Ferrufino & Lapointe 1989), and we have observed high levels of damage to this grass from spittlebugs in Colombia and Central America.

A mass-rearing technique for the spittlebugs *Zulia colombiana* F. and *Aeneolamia varia* (F.) (Lapointe et al. 1989b) and a bioassay (Ferrufino & Lapointe 1989) have been developed to screen CIAT's collection of *Brachiaria* germplasm for sources of host plant resistance. Initial efforts were concentrated on identification of well-adapted accessions from field collections for immediate cultivar introduction. All important cultivated species of *Brachiaria* are apomictic

making intraspecific as well as interspecific crosses equally difficult. However, identification of sexual *B. ruziziensis* Germain & Evrard (Ferguson & Crowder 1974) and induction by colchicine of tetraploid *B. ruziziensis* (Gobbie et al. 1983) have made possible hybridization between induced tetraploid *B. ruziziensis* and natural tetraploid apomicts (*B. brizantha*, *B. decumbens*, *B. jubata* (Fig. & De Not.) Stapf, and others). This makes possible interspecific crosses using sexual *B. ruziziensis* as a bridge.

Here we report results of screening of CIAT's forage germplasm collection for antibiotic resistance in accessions of *Brachiaria* to the spittlebug *A. varia* and the identification of new sources of resistance in accessions of *B. jubata*.

Materials and Methods

Screen for Antibiotic Resistance to Spittlebug. Accessions of *Brachiaria* were collected in Africa and transferred by tissue culture to the germplasm bank at CIAT, Palmira, Colombia (Schultze-Kraft et al. 1987). Upon completion of quarantine, accessions were established in the field at Santander de Quilichao (Cauca, Colombia) and propagated vegetatively. For greenhouse trials, stems of *Brachiaria* accessions were planted in 12.7-cm plastic pots filled with sterilized soil (pH 4.8) and fertilized with the equivalent of 50 kg/ha each of N, P, and K. *A. varia* were reared and eggs were obtained from a glasshouse colony as described by Lapointe et al. (1989b). The technique described by Ferrufino & Lapointe (1989) was adapted to screen a large collection of *Brachiaria* for resistance to species of spittlebug. Initially, the spittlebug *Z. colombiana* was used as it occurs in the Cauca valley near CIAT headquarters. Subsequent establishment of a colony of *A. varia* permitted the use of this species which we believe to be the predominant species causing damage to *Brachiaria* in the important cattle-producing area of the savannas of Colombia and Venezuela. At planting, pots were fitted with an aluminum cover with a central 4-cm circular opening through which the grass plants emerged. The cover served to stimulate proliferation of secondary roots at the soil surface as feeding sites for early instars. Two months after planting, each pot was infested with 10 mature *A. varia* eggs previously incubated in the laboratory. By careful selection of fully developed eggs, we typically obtained 100% eclosion within 24 h. When nymphs reached fifth instar, the aluminum cover was removed and an organdy mesh cage was placed over each plant to collect emerging adults.

Infested plants were arranged in a glasshouse in a completely randomized design with 10 replicates. During the experimental period, temperature in the glasshouse fluctuated in synchrony with photoperiod between 19 and 27°C with a mean of $23.2 \pm 1.2^\circ\text{C}$. Relative humidity ranged

between 60% and 90% with a mean of 82%. Accessions included 'Basilisk' (susceptible), 'Llanero' (susceptible, tolerant), and 'Marandu' (resistant, antibiotic) (Ferrufino & Lapointe 1989). Results reported here were obtained with *A. varia*. Because the species-level taxonomy of Latin American cercopids is uncertain and in need of review, voucher specimens have been placed in CIAT's insect collection.

For convenience, *Brachiaria* accessions were screened in four cohorts for a total of 174 accessions; each cohort included 'Basilisk', 'Marandu', and 'Llanero'. Pots were checked daily for mortality of *A. varia*. Adult emergence for each pot and duration of the nymphal period for each emerged adult were recorded. Accessions were selected as resistant if mean adult emergence on that accession was less than the mean adult emergence plus one standard deviation of the resistant check ('Marandu') of the respective cohort. Survival days were calculated as the number of days nymphs survived from the egg stage when reared on each accession.

Stage-Specific Mortality Curves. Twelve pots each of six accessions were infested with 10 fully developed eggs of *A. varia* in the glasshouse: 'Basilisk', 'Llanero', 'Marandu', *B. brizantha* CIAT 16338, *B. jubata* CIAT 16531, and *B. jubata* CIAT 16203. Empty egg chorions were retrieved 72 h after infestation along with eggs that had not eclosed. Spittle masses were examined daily for presence of exuviae. Nymphal survival and instar were recorded for each insect until adult emergence was complete.

Mortality of Late Instars on *B. jubata* CIAT 16203. Mortality during early instars was high among nymphs reared on *B. jubata* CIAT 16203. Because early instars underwent rapid decomposition after they died in pots, it was not possible to observe symptoms associated with mortality. To observe the effect of this accession on development of late instars, third and fourth instars of *Z. colombiana* were collected from pastures of 'Basilisk' at Santander de Quilichao and placed on either *B. jubata* CIAT 16203 or 'Llanero' in pots in the glasshouse as above. Thirty nymphs were transferred to three pots of 'Llanero' (10 per pot), and 33 nymphs were transferred to three pots of *B. jubata* CIAT 16203. Survival was recorded daily for each insect until adults emerged or died.

Feeding Rate and Assimilation Efficiency of Adult Spittlebugs. Liquid excreta of adult spittlebugs was collected and measured by caging spittlebugs in parafilm (American Can Company, Greenwich, Conn.) sachets as described by Pathak et al. (1982). Newly emerged adult female spittlebugs (*A. varia*) from our glasshouse colony were collected directly from the spittle mass of the last instar and placed in organdy cages on potted plants of the respective *Brachiaria* accession on which they would be tested. After 3 d,

Table 1. Mean adult emergence and period of nymphal development of *A. varia* reared on controls (cultivars) and selected resistant accessions from four cohorts of *Brachiaria* in a glasshouse*

Cohort	Species	Cultivar or CIAT accession	No. adults emerged	Duration of nymphal stadia, d
I	<i>B. decumbens</i>	Basilisk	8.3 ± 1.5	37.2 ± 3.2
	<i>B. dictyoneura</i>	Llanero	8.0 ± 1.5	39.4 ± 4.5
	<i>B. brizantha</i>	Marandu	0.5 ± 0.7	44.4 ± 3.8
	<i>B. jubata</i>	16531	0.3 ± 0.5	37.7 ± 4.5
	<i>B. brizantha</i>	16767	0.6 ± 1.3	38.8 ± 0.4
	<i>B. brizantha</i>	16777	0.8 ± 1.0	40.4 ± 2.9
	<i>B. humidicola</i>	26156	1.1 ± 1.1	40.7 ± 4.6
II	<i>B. decumbens</i>	Basilisk	7.6 ± 0.2	36.4 ± 3.2
	<i>B. dictyoneura</i>	Llanero	7.7 ± 0.1	37.3 ± 4.0
	<i>B. brizantha</i>	Marandu	3.3 ± 0.2	39.6 ± 4.0
	<i>B. ruziziensis</i>	26163	1.8 ± 0.1	36.5 ± 2.7
	<i>B. decumbens</i>	26185	3.0 ± 0.2	36.7 ± 4.3
	<i>B. decumbens</i>	Basilisk	5.7 ± 2.8	37.6 ± 3.7
	<i>B. dictyoneura</i>	Llanero	5.6 ± 2.9	38.2 ± 3.9
III	<i>B. brizantha</i>	Marandu	0.3 ± 0.7	36.0 ± 4.4
	<i>B. jubata</i>	16203	0.1 ± 0.3	42.0 ± 0.0
	<i>B. decumbens</i>	Basilisk	5.5 ± 2.0	36.2 ± 2.4
	<i>B. dictyoneura</i>	Llanero	6.4 ± 2.0	36.7 ± 2.4
IV	<i>B. brizantha</i>	Marandu	0.5 ± 1.0	41.0 ± 2.6
	<i>B. jubata</i>	16531	0.1 ± 0.3	42.0 ± 0.0
	<i>B. brizantha</i>	16827	1.2 ± 1.0	43.0 ± 4.8
	<i>B. brizantha</i>	16829	0.6 ± 1.0	46.0 ± 3.8
	<i>B. subulifolia</i>	16961	1.4 ± 1.4	45.3 ± 4.3
	<i>B. decumbens</i>	26299	0.6 ± 0.9	39.0 ± 4.9

* Ten plants (replications) per accession were infested with 10 eggs each. For duration of nymphal stadia, replicates are individuals and *N* is equivalent to adult emergence × 10. Values are mean ± SD.

adults were placed individually in parafilm sachets, and the sachets were attached to stems of four accessions of *Brachiaria* ('Basilisk', 'Llanero', 'Marandu', and *B. jubata* CIAT 16531). There were 30 replications for each accession of *Brachiaria*. The sachets were collected 24 h later, weighed, dried, then weighed again to determine the weight of the excreta. Control insects were placed in sealed sachets without food for 24 h but provided with a moistened cotton wool swab. All insects were weighed before and after being placed in sachets.

Assimilation of ingested sap was calculated according to the method of Kahn & Saxena (1984) as $W_1 \times [(C_1 - C_2)/C_1] + (W_2 - W_1)$, where *C* and *W* are control and test insects, respectively, and the subscripts refer to initial (1) and final (2) weights.

Means of duration of nymphal stadia and survival, and feeding and assimilation rates, were subjected to analysis of variance (ANOVA) followed by Duncan's (1955) multiple range test (SAS Institute 1982).

Results

Screen for Antibiotic Resistance to Spittlebugs. Adult emergence of nymphs of *A. varia* reared on susceptible controls ('Basilisk' and 'Llanero') was consistently high relative to the resistant 'Marandu' (Table 1). Although adult emergence varied between cohorts, the relative positions of the controls did not vary, which leads us to conclude that variation between co-

horts was due to differences in the condition of vegetatively propagated plants and environmental conditions in the glasshouse. Accessions identified as resistant, such as *B. jubata* CIAT 16531 and *B. jubata* CIAT 16203, have proven to be consistently resistant in subsequent trials (unpublished data). Therefore, we conclude that the bioassay is accurate in that the relative susceptibility of accessions is consistent between trials, although it is not precise because adult emergence on susceptible accessions varied considerably between trials. Of 174 accessions tested, a total of 11 (6%) was selected from the four cohorts as at least as resistant to *A. varia* as the resistant 'Marandu' based on their performance in this bioassay (Table 1).

Antibiotic Effect of *B. brizantha* 'Marandu'. Survival of nymphs to adult on the resistant 'Marandu' varied between 3 and 33% in the four cohorts for which we report data. In these trials and others we have conducted, there is a tendency for a delay in development time for nymphs reared on 'Marandu' compared with that on 'Basilisk' and 'Llanero' (Table 1). This effect cannot be detected in those accessions where very few nymphs completed development. Nymphs reared on 'Marandu' were frequently observed to leave their spittle mass and wander over the soil surface within the pot, finally dying in a dehydrated condition. Mortality of nymphs reared on 'Marandu' is not associated with molting.

Antibiotic Effect of *B. jubata* CIAT 16531. We observed disruption of molting of nymphs reared on *B. jubata* CIAT 16531. Mortality of late in-

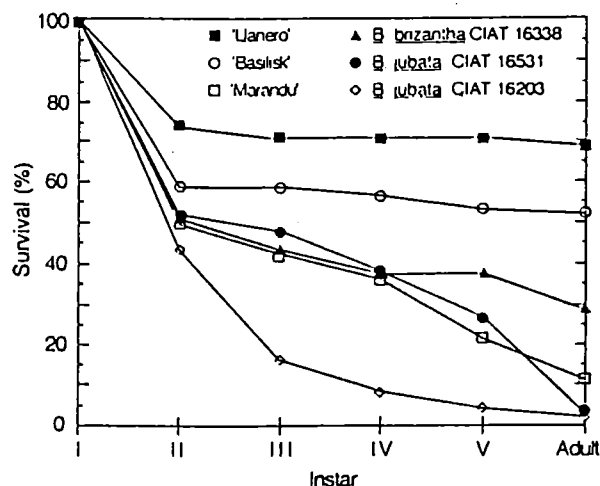


Fig. 1. Survivorship of nymphs of *A. varia* reared on six accessions of *Brachiaria* in a glasshouse. Initial infestation was 10 eggs per plant with 12 replications (plants) per accession.

stars typically occurred after apolysis but before ecdysis could be completed. Many nymphs and pharate adults were observed to die while still encased within the previous nymphal exuviae with the ecdysal suture ruptured. All fourth and fifth instars that failed to survive to adult either died in the pharate condition or died during the process of ecdysis and had wrinkled wings, discoloration, and deformations of the cuticle. In contrast to nymphal mortality on 'Marandu', nymphs reared on *B. jubata* CIAT 16531 typically died within their spittle mass in a fully hydrated state.

Mortality Curves. In all accessions, both susceptible and resistant, considerable mortality occurred during the first-instar stadium, when newly eclosed nymphs were searching for feeding sites and were most susceptible to desiccation (Fig. 1). Presumably, this mortality was independent of host plant. However, on 'Basilisk' and 'Llanero', survival from first instar to adult was essentially 100%. Although both accessions of *B. jubata* were highly resistant in terms of adult emergence, nymphs reared on *B. jubata* CIAT 16531 suffered relatively greater mortality

in late instars, similar to that on 'Marandu'. The mean number of survival days of nymphs reared on 'Llanero' was highest (Table 2), consistent with previous observations that this tolerant cultivar is an excellent host for spittlebugs (Ferrino & Lapointe 1989). Mortality of nymphs reared on *B. jubata* CIAT 16203 was highest in early instars (Fig. 1); that is reflected in the low number of survival days of nymphs reared on this accession (Table 2). *B. brizantha* 16338, highly resistant in the field (Lapointe et al. 1989a), was intermediate in terms of nymphal survival in the glasshouse. This accession has an extreme upright growth habit with narrow leaves that may be responsible for its resistance in the field, perhaps related to low quality of shelter provided to nymphs (McEvoy 1986). As in the case of field resistance to spittlebug in the grass *Andropogon gayanus* (Ferrino & Lapointe 1989), the difference between reaction to spittlebug in the field and in the glasshouse is probably the result of plant architecture, an important characteristic in the field but not detectable by the bioassay used here.

Transfer of Late Instars to *B. jubata* CIAT 16203. Because nymphal mortality was consistently high during early-instar stadia on *B. jubata* CIAT 16203, we were not able to observe molt disruption or other symptoms associated with mortality as seen in nymphs reared on *B. jubata* CIAT 16531. However, when third and fourth instars of *Z. colombiana* were collected from the field and placed on *B. jubata* CIAT 16203, mortality was high compared with nymphs transferred to Llanero (Table 3). Malformed pharate adults resulted from nymphs transferred to *B. jubata* CIAT 16203, similar to symptoms described for nymphs reared on *B. jubata* CIAT 16531. Emergence of normal adults from nymphs transferred to 'Llanero' was 87% (26 of 30) compared with only 6% (2 of 33) of nymphs transferred to *B. jubata* CIAT 16203. No malformations were observed among nymphs transferred to 'Llanero'. The nymphs that died in an apparently normal condition on *B. jubata* 16203 (13 of 33) all died within 4 d of transfer. In four cases (three adults and one nymph), insects reared on *B. jubata* CIAT 16203 showed a peculiar defect upon completion of molt in that both

Table 2. Mean duration of nymphal stadia and mean survival of nymphs of *A. varia* reared from eggs on six *Brachiaria* accessions in a glasshouse

Species	Cultivar or CIAT accession	D to adult emergence	SD (n)	Survival, d	SD (n)
<i>B. dictyoneura</i>	Llanero	35.3b	2.9 (63)	31.1a	3.0 (71)
<i>B. decumbens</i>	Basilisk	33.9c	2.4 (47)	28.6b	3.0 (61)
<i>B. brizantha</i>	16338	38.4a	3.7 (25)	27.0b	6.6 (52)
<i>B. brizantha</i>	Marandu	39.1a	4.0 (12)	22.9c	8.3 (54)
<i>B. jubata</i>	16531	37.3b	2.5 (3)	20.4d	5.1 (55)
<i>B. jubata</i>	16203	33.0c	0.0 (2)	11.5e	3.6 (64)

Means in each column followed by the same letter do not differ ($\alpha = 0.05$, Duncan's [1955] multiple range test).

Table 3. Fate of third and fourth instars transferred from pastures of *B. decumbens* 'Basilisk' and placed on either *B. dictyoneura* 'Llanero' or *B. jubata* CIAT 16203 in a glasshouse

Species	Cultivar or CIAT accession	Initial infestation, n	Normal mortality ^a	No. deformed nymphs ^b	No. normal adults	No. deformed adults ^c
<i>B. jubata</i>	16203	33	13	4	2	14
<i>B. dictyoneura</i>	Llanero	30	4	0	26	0

^a Number of insects that died during nymphal stadia without unusual symptoms.

^b Died during molt to next nymphal instar.

^c Died as deformed adults or as pharate adults unable to shed exuviae.

mandibular and maxillary stylets were curled and located outside the labium.

Adult Feeding Behavior. Adult females produced less excreta and presumably fed less on the antibiotic *B. jubata* CIAT 16531 and 'Marandu' compared with the susceptible 'Basilisk' and the tolerant 'Llanero' (Table 4). Assimilation rate of adult females was significantly less on 'Marandu' compared with females on *B. jubata* CIAT 16531, and the latter was not significantly less than that on the tolerant 'Llanero'.

Discussion

In the absence of a reliable field screening methodology, selection of resistant accessions from germplasm collections has been difficult in years without a sufficient natural infestation of spittlebugs (Lapointe et al. 1989a). As a result, cultivars such as *B. dictyoneura* CIAT 6133 ('Llanero' in Colombia) have been released that are well adapted and productive under grazing but possess limited resistance to spittlebugs (Ferrufino & Lapointe 1989). Furthermore, selection under low to moderate insect pressure in the field and selection on the basis of visual damage have resulted in selection of tolerance rather than antibiosis. Initial crosses of induced tetraploid sexual *B. ruziziensis* and natural tetraploid apomicts have been made at CIAT. Therefore, we initiated a search for sources of antibiotic resistance to spittlebug.

As screening of the *Brachiaria* germplasm collections proceeds, it appears increasingly unlikely that an ideal accession will be found among naturally occurring genotypes that combines edaphic adaptation as well as tolerance to acidity, aluminum toxicity, drought, and resis-

tance to biotic factors. However, we report here 11 accessions from six species of *Brachiaria* that possess high levels of antibiotic resistance to *A. varia*. These may be used as resistance sources in a breeding program. It should be noted that the taxonomic status of species of *Brachiaria* is confused because of the lack of a comprehensive analysis of the genus or of CIAT's recent germplasm collection. Species intergrade morphologically and in many cases, the specific epithet assigned must be considered provisional. Although we report highly resistant accessions of *B. decumbens* and *B. ruziziensis* (species usually considered highly susceptible to spittlebug), the species determination of these accessions is uncertain. For our purposes, we assume that breeding techniques such as embryo rescue will eventually make the entire genus available as a single gene pool. Therefore, resistance to spittlebug will be valuable even if present in poorly adapted species such as *B. jubata*.

Circumvention of apomixis in *Brachiaria* opens the possibility for breeding to improve well-adapted accessions for spittlebug resistance. As suggested by Gobbe et al. (1983), the presence of both apomicts and sexual individuals within progenies of sexual crosses of *Brachiaria* will facilitate fixing of characters in heterotic apomictic progeny that can be released as true-breeding cultivars. It should be possible to obtain hybrid vigor (heterosis) in fixed lines without the need to produce hybrid seed. With identification of resistant accessions, breeding may now proceed to improve *Brachiaria* for resistance to spittlebug, its major biological constraint.

There appear to be at least two distinct types of antibiotic resistance toward spittlebugs in *Brachiaria* accessions. In the case of 'Marandu', the resistance is known to be stable and effective against several species and genera of spittlebugs found throughout Latin America (Nilakhe 1987, Ferrufino & Lapointe 1989). Antibiosis in 'Marandu' appears to be the result of a toxin or an antifeedant that deters feeding, leading to death by starvation and desiccation during nymphal stadia. Nymphs that died in this manner showed no evidence of initiation of molt to the next instar. Adults fed less on 'Marandu' compared with susceptible 'Basilisk' and 'Llanero', and assimilation was low.

Table 4. Excretion rate and assimilation rate during 24 h of 3-d-old adult *A. varia* caged on four accessions of *Brachiaria*

Species	Cultivar or CIAT accession	Excretion rate, ml/d	Assimilation rate, mg/d
<i>B. jubata</i>	16531	219.1a	5.2a
<i>B. decumbens</i>	Basilisk	878.7b	4.6ab
<i>B. dictyoneura</i>	Llanero	893.1b	5.2a
<i>B. brizantha</i>	Marandu	389.8a	3.5b

Means in each column followed by the same letter do not differ ($\alpha = 0.05$, Duncan's [1955] multiple range test).

In the case of *B. jubata* CIAT 16531 and 16203, molting was disrupted; an insect growth regulator may be involved. The presence in a wide range of lower and higher plants of compounds that mimic the action of the insect molting hormone ecdysone has been well documented (Bergamasco & Horn 1983). Phytoecdysteroids have been shown to produce a variety of symptoms when ingested by insects or applied topically (Sato et al. 1968). Symptoms observed in nymphs reared on *B. jubata* CIAT 16531 and CIAT 16203 agree with the physiological action of ecdysone analogues described by Sláma (1969); that is, stimulation of ecdysial processes without synchronization with other developmental processes resulting in precocious molts or inability to shed the exuviae. However, at this point, other possible agents such as juvenile hormone analogues or unique compounds cannot be discarded. What we have observed appears to be disruption of molting, a complex event that consists of several distinct processes. As Kubo & Klocke (1986) point out, ecdysis may be inhibited by ecdysone, juvenile hormone, or their respective analogues (both artificial and from plant sources), or by unique plant compounds.

Although adults fed less on *B. jubata* CIAT 16531, assimilation was high, equal to the susceptible controls. We have no explanation for this effect other than it may be related to the mechanism of resistance of this accession, i.e., a putative hormonomimetic effect that interferes with molting but that would not have an obvious effect on host plant quality for adults. We plan to proceed with a bioassay-directed search for activity in chemically defined plant fractions in an attempt to identify biochemical mechanisms of action present in accessions of *Brachiaria*.

Acknowledgment

We are grateful to C. Cardona and A. C. Bellotti (Centro Internacional de Agricultura Tropical) for critical review of this manuscript.

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Received for publication 14 March 1991; accepted 21 February 1992.

Manejo de dos plagas clave para forrajes de las sabanas neotropicales

S. L. Lapointe*

Introducción

Las sabanas neotropicales representan una amplia frontera agrícola para el continente. Las gramíneas del género *Brachiaria* han sido clave en el desarrollo de la ganadería de esta zona, debido a su excelente adaptación a los suelos ácidos de baja fertilidad. Además de su importancia en la alimentación animal, *Brachiaria* es importante en sistemas de producción de cultivos. En los suelos frágiles de las sabanas tropicales, los monocultivos no mantienen su productividad. Sin embargo, en estos suelos la rotación del cultivo de arroz con especies de *Brachiaria* tienen un alto potencial para mantener la estructura y mejorar la fertilidad del suelo, e inclusive, para aumentar el rendimiento del arroz.

Desafortunadamente, tanto el arroz como las variedades comerciales de esta gramínea son susceptibles a dos plagas importantes que, en parte, caracterizan las sabanas de América del Sur: las hormigas arrieras y los cercópodos (salivazo o mión de los pastos). Debido a la importancia que el sistema de cultivo arroz-pastos tiene en esta región, el manejo de estas plagas es importante para mantener la producción agropecuaria.

En este artículo se resumen las experiencias del autor sobre el control de cercópodos y hormigas arrieras, utilizando la resistencia varietal de *Brachiaria* y algunos métodos culturales.

Cercópodos

La productividad y la persistencia de las pasturas de *Brachiaria* son limitadas en América Latina por su susceptibilidad a un complejo de especies nativas de cercópodos de los géneros *Aeneolamia*, *Delassor*, *Deois*, *Mahanarva*, *Prosapia*, *Sphenorhina*, *Tomaspis* y *Zulia*. Aunque *B. decumbens* cv. Basilisk (CIAT 606) es muy susceptible al daño por cercópodos, es la variedad más común, debido a sus buenas características agronómicas y a su adaptación a suelos de baja fertilidad. En Brasil, se lanzó en 1984 la variedad *B. brizantha* cv. Marandú (CIAT 6294, 6297 y 6780), que tiene resistencia tipo antibiosis a cercópodos (Ferrufino and Lapointe, 1989); sin embargo, Marandú es exigente en nutrientes y, en consecuencia, sólo se cultiva en suelos de mayor fertilidad. Recientemente, *B. dictyoneura* cv. Llanero (CIAT 6133) se liberó en Colombia debido a su tolerancia al daño por cercópodos y su compatibilidad con leguminosas forrajeras; pero se ha demostrado que este cultivar es un excelente hospedero para las ninfas de este insecto (Ferrufino and Lapointe, 1989), los cuales ocasionan daños significativos en pasturas de esta especie en Colombia y América Central.

Además del daño a la pastura, los cercópodos pueden causar daño en el cultivo de arroz ya que, bajo ciertas circunstancias, los insectos prefieren este cultivo y pueden migrar hacia él (Nilakhe, 1985; Parada y Vargas, 1985). Por lo tanto, la asociación de arroz con especies de *Brachiaria* susceptibles a cercópodos puede resultar perjudicial. En consecuencia, es necesario desarrollar nuevas variedades de *Brachiaria* resistentes a cercópodos que inhiban el desarrollo del insecto (resistencia tipo antibiosis).

* Entomólogo, Ph.D., Programas de Arroz y Forrajes Tropicales, Centro Internacional de Agricultura Tropical (CIAT), Apartado aéreo 6713, Cali, Colombia.

Historia de *Brachiaria* en el Nuevo Mundo

Todas las variedades comerciales de *Brachiaria* tienen grandes limitaciones bióticas o abióticas, siendo la principal su susceptibilidad a cercópodos. Las primeras introducciones de esta gramínea al Nuevo Mundo ocurrieron durante los siglos 18 y 19, época en la cual se utilizaba *B. mutica* en los barcos que transportaban esclavos (Figura 1). En 1952, la FAO introdujo a Belém, Brasil, la variedad *B. decumbens* cv. Basilisk, y en 1965 se introdujeron variedades de *B. brizantha* y *B. ruziziensis*.

Mientras que las dos últimas especies no se propagaron debido a su escasa adaptación a suelos pobres, *B. decumbens* cv. Basilisk, por el contrario, mostró excelente adaptación edáfica y se ha multiplicado ampliamente por toda América Latina. Sin embargo, su productividad es limitada en forma severa por el ataque de

especies de insectos de la familia Cercopidae. *Brachiaria humidicola* CIAT 679 (cv. Pasto Humidicola en Colombia, y cv. Común en otros países) se seleccionó por su tolerancia a cercópodos y reemplazó a *B. decumbens* en muchas zonas tropicales. Pero las altas poblaciones de este insecto y los daños severos que, a veces, ocasionan en *B. humidicola*, han creado la necesidad de identificar resistencia tipo antibiosis, para evitar el incremento de la población del insecto, lo que frecuentemente se asocia con tolerancia. Por otra parte, *B. brizantha* cv. Marandú se ha adoptado en muchas regiones por su alto nivel de resistencia tipo antibiosis a cercópodos, pero requiere suelos de mayor fertilidad, en comparación con *B. decumbens* cv. Basilisk. En resumen, hoy en día, a pesar de las distintas variedades comerciales de *Brachiaria* disponibles, todas tienen grandes limitaciones, bien sea de adaptación a suelos de baja fertilidad o por el ataque de plagas (Recuadro 1).

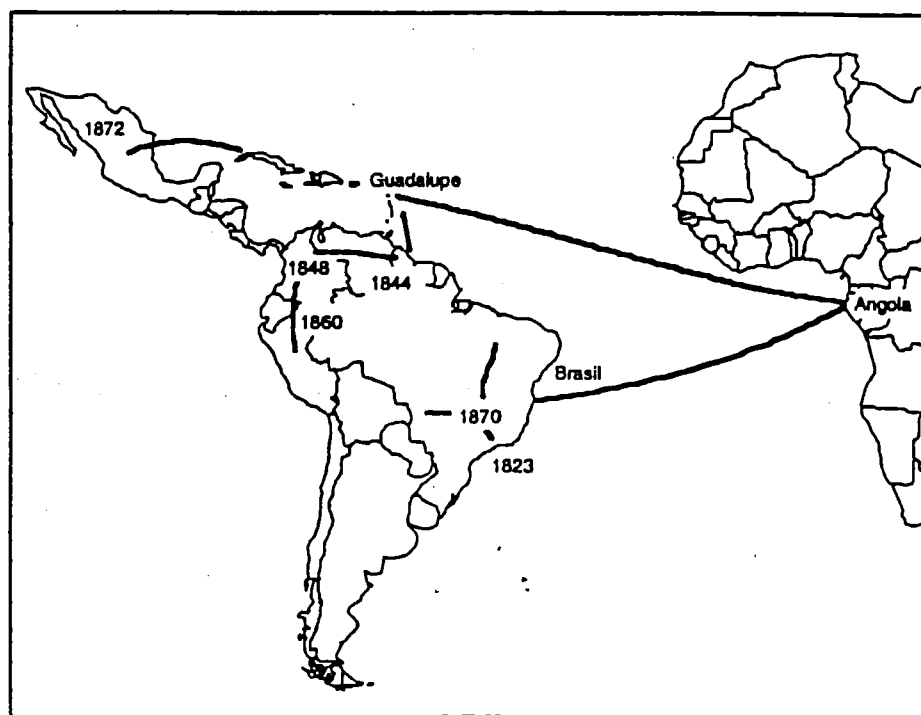


Figura 1. Rutas probables de introducción de *Brachiaria* en América.

FUENTE: Parsons, 1972.

Recuadro 1. Limitaciones bióticas y abióticas de los cultivares comerciales de *Brachiaria* y de *Andropogon gayanus*, promisorios para los Llanos Orientales de Colombia.

Especie o cultivar	Características principales
<i>A. gayanus</i> Carimagua-1	Adaptado a suelos ácidos. Resistente a cercópodos. Altamente susceptible a hormigas arrieras.
<i>B. brizantha</i> Marandú	Resistente a cercópodos (antibiosis). Adaptación edáfica regular. Persistencia limitada. Resistente a hormigas arrieras. Tetraploide, apomíctica.
<i>B. decumbens</i> Basilisk	Adaptada a suelos ácidos. Resistente a la sequía. Susceptible a cercópodos. Resistente a hormigas arrieras. Tetraploide apomíctica.
<i>B. dictyonera</i> Llanero	Tolerante/susceptible a cercópodos. Susceptible a hormigas arrieras. Hexaploide, apomíctica.
<i>B. humidicola</i> Pasto Humidicola	Tolerante a cercópodos. Baja calidad. Resistente a hormigas arrieras. Hexaploide, apomíctica.

La colección de germoplasma de *Brachiaria* en el CIAT

Teniendo en cuenta la importancia de *Brachiaria* y el hecho de que todas las variedades comerciales tienen limitaciones, entre 1984 y 1985 el CIAT hizo una recolección de germoplasma de este género en varios países del Africa, con el fin de ampliar los recursos genéticos que permitan solucionar estos problemas. La colección existente en el CIAT tiene unas 685 accesiones de 26 especies de *Brachiaria* (Torres et al., 1993). De igual manera, en varios países de América Latina se han evaluado colecciones de *Brachiaria*, lo que ha permitido identificar accesiones promisorias por su resistencia a cercópodos y por su adaptación a condiciones adversas de clima y suelos. Algunas de estas accesiones se están evaluando con animales en pastoreo.

Cría masiva de cercópodos

Lapointe et al. (1989 y 1990a) desarrollaron un método que permite la cría masiva de

cercópodos. La técnica consiste en sembrar tallos de una accesión susceptible de *Brachiaria* en macetas de plástico, que se cubren con una tapa de aluminio. Esta última provee condiciones de humedad relativa y baja radiación solar y, a la vez, estimula la proliferación de raíces superficiales como sitios de alimentación para las ninfas en los primeros estadios. Actualmente, la colonia de *Aeneolamia varia* existente en el CIAT produce semanalmente entre 50,000 y 100,000 huevos viables.

Bioensayo para medir antibiosis

Para evaluar la colección de germoplasma de *Brachiaria* existente en el CIAT, se utilizó como bioensayo el método de cría masiva (Ferrufino and Lapointe, 1989). El objetivo fue identificar fuentes de resistencia varietal hacia cercópodos para un posible programa de mejoramiento. Así, se han logrado identificar varias accesiones de diferentes especies con resistencia tipo antibiosis (Lapointe et al., 1992) (Figura 2). La resistencia se caracteriza por una baja supervivencia de las ninfas a medida que avanzan hacia el estado adulto. Este tipo de resistencia se prefiere porque limita el crecimiento de las poblaciones del insecto y minimiza la emergencia de los adultos; por lo tanto, la migración de éstos hacia cultivos vecinos como el arroz, también se reduce. En contraste, las variedades tolerantes (cv. Llanero y cv. Pasto Humidicola) soportan altas poblaciones, las cuales sí pueden migrar.

Mejoramiento de *Brachiaria*

La mayoría de las especies cultivadas de *Brachiaria* es apomíctica y como tal producen semilla en forma asexual, lo que hace imposible utilizarlas en cruzamientos. Sin embargo, *B. ruziziensis* es sexual y diploide, siendo posible cruzarla, luego de un tratamiento con colchicina para duplicar su número de cromosomas, con accesiones apomícticas y tetraploides como *B. brizantha* o *B. decumbens* (Ferguson and Growder, 1974; Gobbe et al., 1983).

En 1993, se sembraron para evaluación posterior en el campo, progenies de cruces que, por primera vez, combinaron genes de *B. decumbens* cv. Basilisk —de buena adaptación a suelos de baja fertilidad— con *B. brizantha* cv. Marandú —con resistencia tipo antibiosis a cercópodos. Estas progenies se evaluaron en el

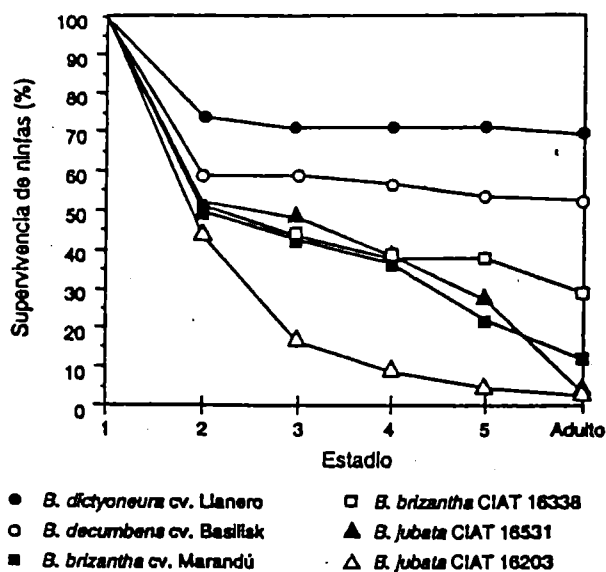


Figura 2. Efecto de seis accesiones de *Brachiaria* sobre la supervivencia de ninfas de *Aeneolamia* varia. Nótese el efecto antibiótico de *B. brizantha* cv. Marandú y de las dos accesiones de *Brachiaria* jubata.

FUENTE: Lapointe et al., 1992.

campo y en casa de vidrio en el CIAT para seleccionar las primeras variedades resultantes de la hibridación de *Brachiaria* (Lapointe and Miles, 1992).

Control cultural de cercópodos

En Campo Grande, Brasil, Koller e Valério (1988) demostraron la importancia que tiene el manejo de pasturas para el control de cercópodos. El pastoreo adecuado, que reduce la biomasa disponible y evita la acumulación de hojas secas y material orgánico, puede controlar parcialmente las poblaciones de cercópodos, debido a la exposición de las ninfas a la disecación por el sol. Debido a que el daño causado por cercópodos en la pastura sólo se visualiza dos semanas después del pico poblacional de las ninfas, es necesario conocer con anticipación las poblaciones emergentes de éstas, lo que dificulta la implementación de este método de control como curación, por lo menos en sistemas extensivos de pastoreo. En consecuencia, se sugiere el uso del pastoreo estratégico como un control preventivo.

Resumen del manejo de cercópodos en pasturas y en sistemas de cultivo arroz-pastos

- (1) Aunque los cercópodos generalmente no cumplen su ciclo de vida en el arroz, los adultos pueden migrar desde pasturas susceptibles causando daños significativos en este cultivo.
- (2) Durante los picos de población del insecto, el pastoreo estratégico puede ayudar a bajar la densidad de las ninfas de cercópodos. Se debe prestar especial atención a las pasturas de gramíneas susceptibles, ubicadas cerca a un cultivo de arroz.
- (3) Se han encontrado altos niveles de resistencia tipo antibiosis en *B. brizantha* cv. Marandú. Sin embargo, otras características, como su escasa adaptación a suelos pobres, limitan la utilización de este cultivar.
- (4) Las progenies resultantes de los primeros cruzamientos entre *B. decumbens*, *B. brizantha* y *B. ruziziensis*, se están seleccionando por adaptación edáfica y resistencia a cercópodos, entre otras características. Se espera que próximamente estarán disponibles nuevas variedades e híbridos de *Brachiaria* para evaluación bajo pastoreo. Estas variedades resistentes deben ofrecer la solución definitiva al problema de cercópodos en pasturas solas y asociadas con arroz, especialmente en los Llanos Orientales de Colombia.

Hormigas arrieras

Las hormigas cortadoras de hojas tienen una presencia biótica dominante en las sabanas de Colombia, Venezuela y los Cerrados de Brasil. Además de su influencia en la composición botánica de la sabana (Elter y Botero, 1990), se estima que las colonias de *Acromyrmex landolti* son capaces de excavar, durante dos meses de la época seca, hasta 1.5 m³ de suelo/ha, lo que indica que también pueden afectar las características físicas del suelo (Lapointe et al., 1990b). Debido a su gran variedad de hospedantes —desde pasturas hasta cultivos de arroz— son una plaga importante y un obstáculo para la explotación agrícola y ganadera de las sabanas (Robinson and Fowler, 1982).

En los Llanos Orientales de Colombia existen por lo menos tres especies de hormigas trozadoras: (1) *Atta cephalotes*, se encuentra principalmente en los bosques de galería y corta únicamente plantas de hoja ancha, como árboles y arbustos; se convierte en plaga sólo cuando se siembran cultivos susceptibles en su medio ambiente. (2) *Atta laevigata*, habita la sabana abierta y corta tanto gramíneas como vegetación de hoja ancha. Construye hormigueros grandes hasta de 10^6 individuos, con numerosas cámaras que alcanzan hasta 5 m de profundidad. (3) *Acromyrmex landolti*, corta gramíneas solamente y construye numerosos nidos, aunque relativamente pequeños (10^4 individuos) en la sabana abierta. Presenta polimorfismo, pero no es tan extremo como en *Atta* y no posee una casta de soldados. Las obreras de *A. landolti* no construyen los caminos que son notables en el caso de *Atta*. Los nidos de *A. landolti* son pequeños y alcanzan altas densidades en la sabana nativa, llegando hasta 2000 nidos/ha. Los hormigueros de esta especie pueden tener entre tres y 10 cámaras de poco volumen (una cámara típica ocupa 500 cm^3). Por lo general, estas cámaras se ubican en forma vertical bajo el suelo. En los Llanos Orientales de Colombia, cada hormiguero presenta una sola entrada (Lapointe et al., 1993). Aparentemente, los hormigueros de *A. landolti* no permanecen en un solo sitio por más de un año, lo que hace suponer que las hormigas pueden mudarse y establecerse en otro sitio, aunque es poco lo que se conoce de este comportamiento.

Los hormigueros de *A. laevigata* y *A. cephalotes* pueden cubrir varios metros cuadrados de superficie. Ambas especies presentan un polimorfismo marcado e inclusive tienen una casta de soldados. El control de estas hormigas se simplifica debido al gran tamaño de sus nidos y a su baja densidad por hectárea. Los métodos comunes de control consisten en insuflar los nidos con productos específicos y utilizar cebos tóxicos con base en insecticidas persistentes.

Daños causados por las hormigas arrieras

En arroz, el daño por *A. landolti* se presenta durante la fase de establecimiento. En las pasturas, el daño puede ocurrir en cualquier etapa de desarrollo del cultivo; durante el

establecimiento, el daño es ocasionado por las hormigas de las colonias presentes en el sitio antes de la siembra. La colonización de hormigas arrieras puede ocurrir durante varios años y resultar en la pérdida total de la biomasa.

Durante la germinación, el daño en el cultivo se nota por la presencia de plántulas trozadas, lo cual implica la pérdida de la planta, resultando en un establecimiento incompleto del cultivo. En el arroz, el vigor de la semilla y la fertilización en la siembra permiten la recuperación de las plántulas después del corte ocasionado por las hormigas. Sin embargo, los cortes sucesivos causan la muerte de aquéllas.

Densidad de las colonias de hormigas

Los conteos de colonias en sabana nativa y en gramíneas introducidas sugirieron que algunas variedades de gramíneas del género *Bracharia* son resistentes a *A. landolti* (Lapointe et al., 1990b). El promedio de colonias de esta hormiga en sabana nativa fue de 567 ($n = 136$ observaciones), alcanzando, en algunos casos, hasta 4000 colonias/ha. En contraste, en *Andropogon gayanus* cv. Carimagua-1, la densidad fue superior a 5000 colonias/ha. En *B. humidicola* cv. Pasto Humidicola no se encontraron colonias de la hormiga.

Las observaciones también mostraron que hay una alta variabilidad en la densidad de colonias de *A. landolti* en la sabana y que existen zonas de baja densidad, en las cuales es posible establecer con éxito gramíneas susceptibles. Por tanto, se decidió desarrollar un método para estimar poblaciones en las áreas destinadas a la siembra, determinar un umbral de acción para *A. gayanus* y caracterizar la resistencia o susceptibilidad de otras gramíneas comerciales.

Umbral de acción para *Andropogon gayanus*.

En 1980, el Instituto Colombiano Agropecuario (ICA) liberó *Andropogon gayanus* como cultivar Carimagua-1. En esa época no se reconocía su susceptibilidad a plagas. Sin embargo, a través de los años se ha documentado el tremendo daño que *A. landolti* causa a esta gramínea (Lapointe et al., 1990b). Durante el establecimiento, las plántulas de este cultivar son muy susceptibles al corte ocasionado por

hormigas. En ensayos de establecimiento de *A. gayanus* en áreas de sabana nativa altamente infestadas con *A. landolti*, las pérdidas de plántulas pueden llegar hasta 98%. Cuando la pérdida de plántulas es de 50% o más, el daño en el establecimiento implica la pérdida total de la siembra, siendo necesario sembrar de nuevo o abandonar el lote. En Brasil también se han reportado daños severos en *A. gayanus* por esta plaga (J. R. Valério, comunicación personal).

En la sabana nativa del departamento del Meta, Colombia, las observaciones en hormigueros de *A. landolti* mostraron que la densidad de las colonias de esta especie varía significativamente (Lapointe et al., 1990b). Una estrategia para evitar el daño en gramíneas susceptibles debe involucrar el uso estratégico de las gramíneas disponibles, con base en una evaluación previa de la densidad de los hormigueros en el sitio de siembra y en el conocimiento de la susceptibilidad relativa de esas gramíneas. Así, en la sabana nativa, antes de la preparación del suelo, se encontró que una densidad de 400 hormigueros/ha permitió el establecimiento mínimo de una macolla/m² de *A. gayanus* cv. Carimagua-1.

En el Centro de Investigaciones Carimagua, se determinó que la distribución espacial de los hormigueros de *A. landolti* puede ser altamente agregada y esta agregación está determinada por la microtopografía de la sabana. Aparentemente, la topografía se asocia con la escorrentía del agua durante y después de las lluvias, siendo, probablemente, un factor de mortalidad importante para esta hormiga. Debido a que la agregación espacial puede ser muy pronunciada, se recomienda contar los hormigueros presentes en cuadrantes de 2 m x 100 m, orientados en forma perpendicular a la pendiente del terreno; de esta forma, se reduce la varianza asociada con la distribución (Serrano et al., 1993).

En Carimagua también se encontró que el drenaje influye en la densidad de los hormigueros de *A. landolti* (Lapointe et al., 1990b). En sitios mal drenados, como son los "bajos", o en sitios frecuentemente encharcados, la densidad de colonias de la hormiga fue baja, en comparación con las áreas bien drenadas. Por lo tanto, para realizar un muestreo representativo en áreas de sabana nativa, se recomienda hacer una caracterización de acuerdo con su drenaje.

Resistencia varietal de *Brachiaria* a *Acromyrmex landolti*

Algunas variedades de *Brachiaria* son altamente resistentes a *A. landolti*. Esta resistencia se manifiesta por una reducción en el número de plántulas que sufren corte durante el establecimiento (Figura 3) y en la tasa de colonización de las pasturas establecidas (Figura 4).

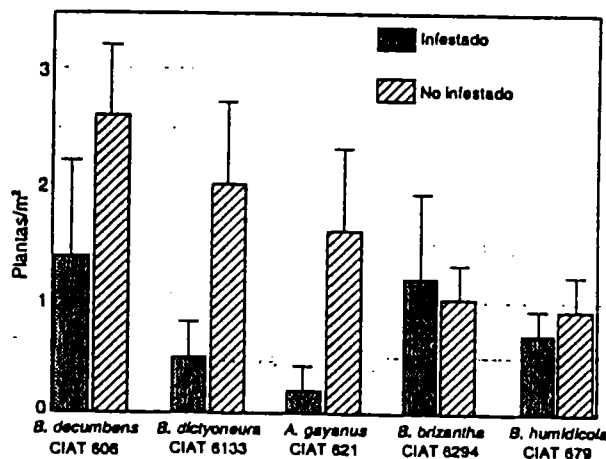


Figura 3. Efecto de la hormiga cortadora (*Acromyrmex landolti*) en el establecimiento de variedades comerciales de *Brachiaria* en el CI. Carimagua, Llanos Orientales de Colombia.

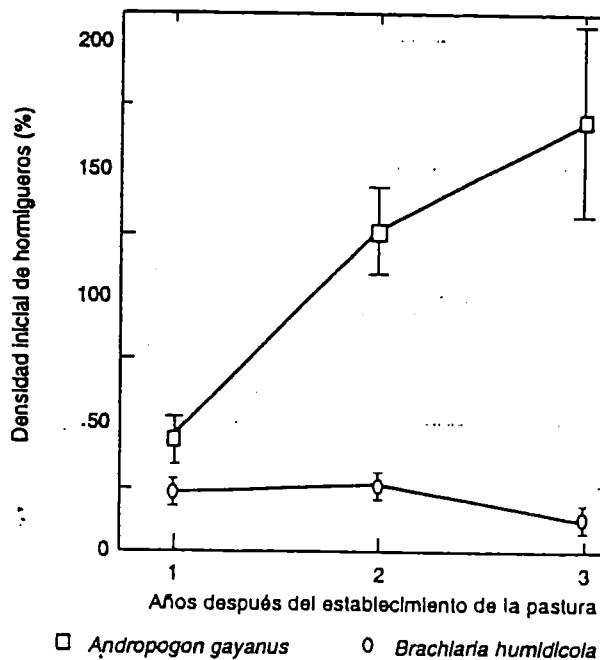


Figura 4. Colonización de pasturas de *Andropogon gayanus* y de *Brachiaria humidicola* por *Acromyrmex landolti*, en franjas de 30 m x 60 m. CI. Carimagua, Llanos Orientales de Colombia.

Cuadro 1. Cultivares comerciales de gramíneas forrajeras y su reacción a la hormiga arriera *Acromyrmex landolti* durante el establecimiento, después del establecimiento (colonización), y como sustrato para el hongo simbiótico *Attamyces bromatificus*.

Cultivar	Establecimiento	Colonización	Sustrato del hongo
<i>A. gayanus</i> cv. Carlomagua-1	S	S	S
<i>Brachiaria dictyoneura</i> cv. Llanero	S	S	S
<i>Brachiaria decumbens</i> cv. Basilisk	MR	R	R
<i>Brachiaria brizantha</i> cv. Marandú	R	R	R
<i>Brachiaria humidicola</i> cv. Pasto Humidicola	R	R	MR

S = Susceptible. MR = Resistencia moderada. R = Resistente.

Este mecanismo de resistencia se debe a que la gramínea inhibe el hongo *Attamyces bromatificus*, simbiótico de la hormiga. En cinco variedades comerciales se encontró concordancia entre la resistencia en el campo y la inhibición del hongo en cultivo sobre agar (Cuadro 1). Esta inhibición del hongo hace posible un bioensayo sencillo para identificar materiales resistentes y para determinar la base bioquímica de la resistencia.

Control cultural de colonias de *Acromyrmex landolti*

La preparación del suelo causa una alta mortalidad de las colonias de *A. landolti* (Lapointe et al., 1990b). En los estudios sobre el comportamiento de las colonias, por medio de excavaciones para determinar la profundidad de las cámaras a través de las épocas del año (Figura 5), se encontró que durante la época seca las cámaras pueden alcanzar una profundidad de 2 m, mientras que en los meses lluviosos las cámaras se concentran en los primeros 25 cm del suelo. Sin embargo, hasta el momento no se ha establecido si la época de preparación del suelo tiene influencia en el control de las colonias.

Costo del control de *Acromyrmex landolti*

El costo aproximado del control químico de colonias *A. landolti* en áreas de sabana nativa, previo a la preparación del suelo, aparece en el Recuadro 2. El control se hizo con clorpirifos (polvo con 2.5% de i. a.) en un promedio de 1000 hormigueros/ha, anotando el tiempo y la

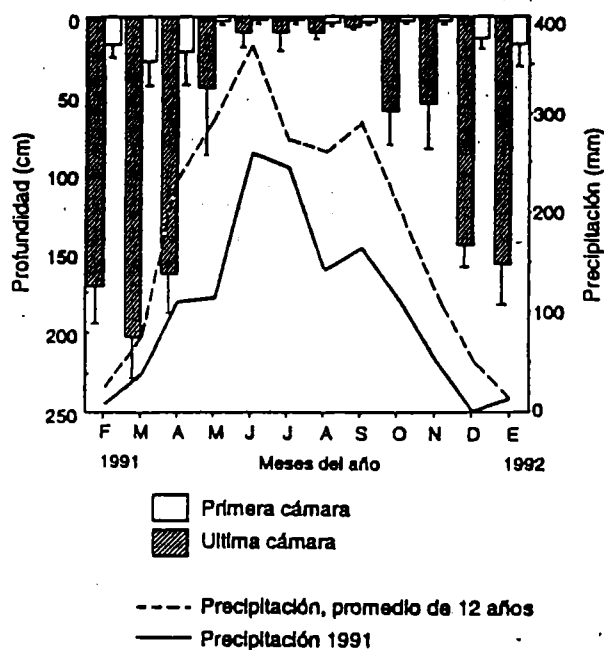


Figura 5. Profundidad de las cámaras de *Acromyrmex landolti* a través de la época del año y su relación con la precipitación. Cl. Carlomagua, Llanos Orientales de Colombia.

cantidad de producto utilizado. Se observa que el costo varía de acuerdo con la experiencia de los operarios, siendo de US\$ 11/ha cuando se hace con trabajadores experimentados y de US\$ 20/ha cuando éstos no tienen experiencia.

Manejo de *Acromyrmex landolti* en pasturas y en sistemas de cultivo arroz-pastos

A continuación se resumen algunas prácticas útiles para el manejo de *A. landolti*:

Recuadro 2. Costo del control químico de colonias de *Acromyrmex landolti* en sabana nativa, antes de la preparación del suelo.

Promedio del tiempo requerido para insuflar una colonia (segundos)	45
Costo de la mano de obra (US\$/jornal)	3.90
Mano de obra usada (jornales/ha)*	de 2 a 3.5
Costo de la mano de obra (US\$/ha)	de 7.80 a 43.65
Cantidad de clorpirifos insuflado/colonia (g)	de 3.1 a 6.3
Costo unitario (US\$/kg)	1.00
Costo del producto (US\$/hormiguero)	de 0.0031 a 0.0063
Costo del control (US\$/ha)*	de 11.00 a 20.00
Umbral de ganancia para el arroz (costo del control/precio del arroz) (kg de arroz 'paddy'/ha)**	de 61 a 111

* Se espera una densidad de 1.000 hormigueros/ha.

** Precio arroz = US\$0.18/kg ('paddy').

(1) Para evitar el daño por *A. landolti* en el cultivo de arroz y en gramíneas susceptibles como *A. gayanus* y *B. dictyoneura*, es importante estimar la densidad de los hormigueros en el sitio de siembra antes de la preparación del suelo. Serrano et al. (1993) diseñaron un método de muestreo de hormigueros, que consiste en:

- Ubicar al azar un punto de partida dentro del área que se va a sembrar.
- Determinar la pendiente general del lote.
- Orientarse perpendicularmente a ella.
- Extender una cuerda o cinta métrica de 100 m de largo.
- Caminar en forma paralela a dicha cuerda o cinta contando, a la ida y al regreso, todos los hormigueros presentes en una franja de 1 m de ancho.
- El número de hormigueros presentes por hectárea se calcula multiplicando por 50 la cantidad de hormigueros presentes en dicha franja.

(2) Para lograr el establecimiento exitoso de una gramínea susceptible, no deben existir más de 400 hormigueros/ha, antes de la preparación del suelo. Si la densidad de hormigueros es mayor, se deben escoger otras alternativas de germoplasma forrajero resistente al ataque de hormigas, tales como *B. brizantha*, *B. decumbens* o *B. humidicola*.

(3) Debido a la rápida e intensa colonización por hormigas de las pasturas de *A. gayanus*, esta gramínea no se recomienda para siembras asociadas con cultivos como arroz, el cual también es susceptible a las hormigas. Las especies resistentes de *Brachiaria* son las

más indicadas para rotaciones y siembras de relevo, por su alta resistencia y su capacidad de eliminar hormigueros.

(4) La identificación del mecanismo de resistencia en *Brachiaria* mediante la inhibición del hongo simbiótico, así como el desarrollo de un bioensayo sencillo aseguran, en el futuro inmediato, la selección de nuevas variedades resistentes.

Conclusión

Aunque los cercópodos y las hormigas arrieras son plagas importantes y con potencial en las sabanas neotropicales, el uso de variedades resistentes de gramíneas forrajeras y prácticas culturales pueden minimizar los daños ocasionados por estos insectos en pasturas y en los sistemas arroz-pastos. El avance en las técnicas que permiten la recombinación genética entre especies de *Brachiaria* ofrece, por primera vez, la posibilidad de combinar características como la resistencia a cercópodos y hormigas arrieras, y la adaptación a suelos infértiles, previamente encontradas en genotipos distintos. El papel de estas nuevas variedades de *Brachiaria* será fundamental para futuros sistemas integrados y sostenibles de cultivos y ganadería en las sabanas de zonas bajas de América tropical.

Summary

Rotations and relay-cropping systems of rice and pastures have demonstrated potential for improving soil fertility, maintaining soil structure and increasing rice yields in the lowland Neotropical savannas. The major components of these cropping systems, rice and forage grasses,

share susceptibility to two major insect pests: species of Cercopidae known as spittlebugs, and leaf-cutter ants (*Atta* and *Acromyrmex* spp.)

This article describes work on the control of these pests through cultural practices and host plant resistance. Management strategies are proposed to minimize losses. Cercopids can be controlled to a limited extent through strategic grazing although the development of resistant hybrid *Brachiaria* cultivars offers the greatest potential for effective control. Resistance to leaf-cutters is also present in the genus *Brachiaria*. Methods to assess populations of leaf-cutter colonies are described as well as damage to susceptible grass cultivars. Estimation of colony density prior to planting is recommended in order to select the proper grass cultivar.

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IMPORTANCIA DE LA COMUNICACIÓN VIBRACIONAL EN EL COMPORTAMIENTO REPRODUCTIVO DEL SALIVAZO DE LOS PASTOS (HOMOPTERA: CERCOPIDAE)

en prensa:

Revista Colombiana de Entomología 2000 vol. 26(1-2)

FRANCISCO LÓPEZ MACHADO¹, DANIEL C. PECK¹ Y JAMES MONTTOYA LERMA²

¹Centro Internacional de Agricultura Tropical (CIAT), Apartado Aéreo 6713, Cali, Colombia

²Universidad del Valle, A. A. 25360 Cali., Cali, Colombia

Resumen. La comunicación por vibraciones a través del sustrato es un aspecto fundamental en el comportamiento reproductivo de los homópteros. Esta forma de comunicación no se había estudiado hasta ahora en la familia Cercopidae. Se determinó el papel que desempeña la comunicación vibracional en el comportamiento reproductivo de *Zulia carbonaria* (Lallemand) y de *Aeneolamia varia* (F.). Los cantos se registraron directamente del sustrato mediante un cartucho fonográfico conectado a una computadora con un programa especializado para el análisis de sonidos. Se realizaron ensayos con machos y hembras, junto con observaciones del comportamiento durante las grabaciones, para determinar la relación entre los cantos y el comportamiento del insecto. Los dos sexos realizaron cantos, aunque el macho fue el que inició la búsqueda de la hembra. Esta forma de comunicación fue fundamental para el apareamiento y el éxito reproductivo en esta familia. Para llamar a la hembra los machos realizaron un canto característico; el de *Z. carbonaria* tenía una frecuencia de 317.38 ± 23.25 Hz y duración de 9.5 ± 0.59 seg, estadísticamente diferente al de *A. varia*, que presentó una frecuencia de 425.16 ± 37.27 Hz y duración de 3.43 ± 0.08 seg. Al detectar el macho emisor, la hembra contestó estableciendo un "diálogo" con el que el macho se orientó hasta encontrarla para iniciar el apareamiento. Se encontraron otros patrones diferentes no relacionados directamente con el apareamiento. Esta es nueva información básica sobre la familia Cercopidae y en especial del salivazo, la plaga más importante en forrajes neotropicales. Considerando las diferencias encontradas en los cantos de las dos especies, se podrían utilizar patrones de comunicación como herramienta taxonómica, como se ha utilizado en otras familias.

Palabras clave: *Aeneolamia varia*. Apareamiento. Bioacústica. Comunicación. Forrajes: Mión de los pastos. Salivazo. Taxonomía. *Zulia carbonaria*.

DESDE EL SIGLO XVIII la comunicación entre los insectos ha sido objeto de estudio en los órdenes Homoptera (Cicadidae) y Orthoptera (Tettigoniidae y Gryllidae) por ser fácilmente audibles sin el uso de equipos especiales. El caso más conocido es el de las cigarras (Homoptera: Cicadidae), cuyos cantos a través del aire pueden escucharse a varios kilómetros de distancia (Kirby y Spence 1818, Alexander 1960, citados por Claridge 1985). La mayoría de los insectos, sin embargo, producen sonidos no audibles para el oído humano. Requieren equipos especiales para poder ser registrados porque en muchos casos se transmiten a través del sustrato como piedras, arena, hojas, tallos e incluso la superficie del agua (Ewing 1989). Esta forma de comunicación se presenta en órdenes como Orthoptera, Blattodea, Isoptera, Plecoptera, Hemiptera, Homoptera, Neuroptera, Coleoptera, Diptera, Trichoptera e Hymenoptera (Stewart 1997).

En el suborden Auchenorrhyncha (Homoptera) se presentan los dos tipos de transmisión: por aire y por el sustrato. Estos cantos son producidos por un órgano situado

dorsolateralmente en el primer segmento abdominal, conocido como timbal (uno a cada lado). A diferencia de la familia Cicadidae, los pequeños homópteros no poseen sacos de resonancia. Por esta razón sus cantos son de baja intensidad (Claridge 1985). Ossianilsson (1949), pionero en realizar estudios sobre comunicación en pequeños homópteros, sugirió que para su comunicación son más importantes las vibraciones a través del sustrato. Propuso un sistema de clasificación de seis tipos diferentes de cantos: 1) canto común ("common song") se realiza de manera espontánea independiente de la presencia de otros insectos, 2) cortejo o apareamiento ("courtship") invita al apareamiento, 3) invitación ("invitation") es producida solo por hembras, 4) agresión ("rivalry") se presenta en caso de competencia por pareja, 5) cópula ("pairing") se realiza durante el apareamiento, y 6) conmoción o alarma ("distress") se produce en situaciones de inconformidad o peligro. Los cantos a través del sustrato alcanzan hasta un metro de distancia (Hunt y Nault 1991).

La comunicación vibracional ha sido una herramienta útil en taxonomía. Claridge y Reynolds (1973) encontraron diferencias en los cantos de cuatro especies del género *Oncopsis* (Homoptera: Cicadellidae) demostrando que funcionan como un mecanismo de aislamiento reproductivo. Claridge *et al.* (1985) en trabajos realizados con dos poblaciones alopatricas de *Nilaparvata lugens* (Stal) encontraron diferencias en la frecuencia de repetición de pulsos (FRP) de sus cantos. Heady *et al.* (1986) realizaron un cladograma con diez especies del género *Dalbulus* basándose en las diferencias de los cantos comunes. Los resultados mostraron tres grupos principales que coincidieron con los tres grupos monofiléticos de la taxonomía obtenidos por morfología.

La comunicación vibracional nunca ha sido estudiada en la superfamilia Cercopoidea (Homoptera). Los estudios de Ossianilsson (1949) y Moore (1961) probaron que las familias Cercopidae, Aphrophoridae y Clastopteridae son capaces de emitir sonidos. Sin embargo, no describieron en detalle las diferentes clases de cantos y no probaron que éstos se transmitieran a través del sustrato. Se desconoce completamente su importancia en el comportamiento reproductivo en la superfamilia Cercopoidea aunque para otras familias como Cicadellidae y Delphacidae son una parte fundamental tanto en el apareamiento, como en el mecanismo de aislamiento reproductivo (Ichikawa 1974, 1976, Heady *et al.* 1986, Hunt y Nault 1991).

En la familia Cercopidae existe un subgrupo formado por algunos géneros que son de importancia económica en cultivos de gramíneas como forrajes y caña de azúcar (Fewkes 1969, Lapointe *et al.* 1994). Este subgrupo se conoce como salivazo o mión de los pastos. La biología de estas especies es bastante desconocida y su taxonomía es muy confusa en la actualidad. El estudio de la comunicación vibracional y el comportamiento relacionado con esta forma de comunicación es importante para ampliar el conocimiento básico de su biología. Además, se abre la posibilidad de utilizar las características de los cantos como herramienta taxonómica.

El objetivo de este trabajo fue comprobar si se presentaba la comunicación a través del sustrato en la familia Cercopidae y determinar su importancia en el comportamiento reproductivo. Se desarrolló una metodología que permitiera grabar los cantos de los adultos directamente del sustrato bajo condiciones que facilitaran la observación al momento de realizar los registros, sin perturbar su comportamiento natural. Esta metodología se usó para obtener evidencia para diferentes clases de cantos en dos especies de salivazo de los pastos: *Zulia carbonaria* (Lallemand) y *Aeneolamia varia* (F.). Se caracterizó en detalle el canto de apareamiento del macho por su relación

directa con el comportamiento reproductivo. Finalmente, se comparó el canto y el comportamiento relacionado entre las dos especies con el fin de encontrar si habían diferencias suficientes para justificar el uso de la comunicación vibracional como herramienta taxonómica en esta familia.

Materiales y Métodos

Sitio y Especies de Estudio

El trabajo se realizó en el Centro Internacional de Agricultura Tropical (CIAT), Palmira, Valle del Cauca. Las condiciones del laboratorio donde se realizaron los registros fueron 23-26°C y 50-64% de humedad relativa.

Se utilizaron dos especies para estudiar la comunicación vibracional en la familia Cercopidae. Inicialmente se eligió a *Z. carbonaria* para el establecimiento de la metodología debido a que es común en los departamentos de Cauca y Valle, es muy dócil y además era la mas grande de la especies disponibles. Esto facilitó su manejo bajo condiciones experimentales, tanto en el establecimiento de una cría, como en la realización de los registros. Para establecer la cría se utilizaron adultos traídos de Santander de Quilichao (Cauca), siguiendo la metodología de cría de *A. varia* descrita por Lapointe *et al.* (1994). *Z. carbonaria* fue erróneamente identificada y conocida en Colombia como *Zulia colombiana*, la cual es un sinónimo menor de *Zulia pubescens* (F.), otra especie presente en la misma zona geográfica (CIAT 1999)

Una vez que se estandarizó la metodología de adquisición se utilizó *A. varia* para registrar y comparar sus cantos con los de *Z. carbonaria*. En Colombia *A. varia* se presenta en los Llanos Orientales y del Piedemonte Amazónico de Colombia. Para estos estudios los adultos se obtuvieron de una cría masiva establecida desde hace diez años en el CIAT, con renovaciones periódicas con insectos traídos del campo desde Meta y Caquetá.

Para los ensayos se utilizaron adultos de 1 – 2 días de edad para reducir fuentes de variación entre individuos como la edad, gravidez de las hembras y el período de precópula. Los adultos tenerales sexados fueron separados en pots con plantas de *Brachiaria ruziziensis* (Germain y Evrard) dentro de cilindros de acetato hasta el momento de realizar los registros.

Montaje para la Adquisición de Registros

Se estableció un montaje que permitiera verificar la existencia de comunicación vibracional entre los cercópidos para su posterior adquisición, análisis y caracterización. Para registrar los cantos directamente del sustrato se utilizó un cartucho fonográfico tipo cristal cerámico (Normarh® Ref.

MIT). Este se sujetó a la punta de una pequeña vara de madera (8.0 cm de longitud y 0.3 cm de diámetro), acoplada a un soporte o "mano auxiliar" (Ref. 12-051 GC Electronics®). Este soporte facilitó mantener el cartucho en contacto permanente con el tallo de la planta, debajo de la última hoja (Fig. 1).

Para todos los ensayos se utilizaron como sustrato tallos de *B. ruziizensis* de 25 - 32 cm de alto, con tres hojas. Este arreglo facilitó al insecto espacio suficiente para caminar, alimentarse e interactuar con otros individuos al tiempo que permitió una distancia máxima de 30 cm con el cartucho (Fig. 1). Este rango aseguró una buena transmisión de las vibraciones del insecto al cartucho. La base del tallo se mantuvo en un recipiente plástico (40 ml capacidad) con agua, tapado con un cilindro de espuma. El tallo de la planta se introdujo por un corte en el centro de la espuma.

El cartucho se conectó mediante un cable blindado a un pre-amplificador (especificaciones no disponibles) construido especialmente para aumentar la señal antes de ser procesada. El cartucho se rodeó con una malla de acero y el resto del montaje con una caja de Faraday fabricada en malla de aluminio conectada a tierra en el amplificador para descargar las interferencias electromagnéticas (Hunt y Nault 1991). Para reducir vibraciones externas el montaje, se instaló sobre una lámina de polipropileno (Icopor) y ésta a su vez sobre una lámina de espuma. Posteriormente (Fig. 1), la señal se almacenó en una computadora (Gateway GP6 450) con una tarjeta de sonido (Sound Blaster PCI 64V) que convertía la señal analógica en una digital para poder realizar los análisis correspondientes.

Para conseguir evidencia para las diferentes clases de cantos, se utilizaron cinco combinaciones de individuos simulando un rango de situaciones naturales: un macho, dos machos, una hembra, dos hembras, y una pareja. Bajo estas circunstancias se hicieron observaciones visuales, junto con los registros, para obtener evidencia de las distintas clases de cantos. Los cantos se distinguieron por los patrones (sonogramas) distintos al ser graficados y por el comportamiento asociado del insecto. No se pretendió cuantificar la actividad bioacústica según especie, sexo u otras condiciones. Se incluyeron todos los registros interpretables para realizar los análisis. Se sometieron aproximadamente 30 adultos de *Z. carbonaria* y 15 de *A. varia*, representando 40 horas de grabación aproximadamente.

Análisis y Caracterización de los Registros

Los análisis de los registros se realizaron utilizando un programa para PC llamado "Cool-Edit." Este programa permitió visualizar los cantos como oscilogramas y como gráficas de análisis de espectro.

Los sonogramas ilustraron la forma de la onda del canto y cómo cambia respecto al tiempo. Las gráficas de análisis de espectro mostraron como cambia la intensidad del canto (medido en decibeles, dB) respecto a la frecuencia. Para caracterizar el canto de apareamiento y los otros cantos, se midieron tres parámetros físicos con el mismo programa: tiempo de duración del canto, frecuencia del canto y frecuencia de repetición de pulsos (FRP). Se definió un pulso como la unidad mínima de repetición en que se pudo dividir el canto. Cuando se obtuvieron múltiples registros en un solo individuo se promediaron y se trataron como una sola repetición.

Se comparó el canto de apareamiento de los machos de *Z. carbonaria* y *A. varia*. Se tuvieron en cuenta los tres parámetros anteriormente descritos: duración, frecuencia y FRP. Las diferencias en los promedios de cada parámetro se detectaron mediante una prueba Tukey con $\alpha = 0.05$.

Resultados

Se obtuvieron registros a través del sustrato para machos y hembras de *Z. carbonaria* y *A. varia*. Con base en los diferentes patrones asociados con su respectivo comportamiento, se obtuvo evidencia para cinco clases de cantos: alarma, común, apareamiento, invitación y otro desconocido.

Caracterización del Canto de Apareamiento

Para realizar una buena caracterización del canto de apareamiento, se lograron once registros en *Z. carbonaria* y cinco en *A. varia*. El canto de apareamiento de *Z. carbonaria* presentó una frecuencia de 317.38 ± 23.25 Hz ($294.13 - 340.63$) con una intensidad mayor (dB) entre 220 y 330 Hz (Figs. 2 y 4a), una duración promedio de 9.5 ± 0.59 seg. ($8.91 - 10.09$) con una FRP de 10.50 ± 0.37 ($10.13 - 10.87$) pulsos por seg. ($n = 11$). Se observó que la amplitud de los pulsos disminuyó y el tiempo entre los mismos aumentó con el transcurso del canto (Fig. 2). Al dividir el canto en cuatro partes iguales, la FRP calculada disminuyó significativamente entre cada una de las cuatro partes: 12.12 ± 0.37 , 11.23 ± 0.37 , 10.78 ± 0.29 , 7.62 ± 0.39 pulsos/seg., respectivamente. Los machos hicieron el canto de apareamiento cuando estuvieron solos o en compañía de otro macho o hembra.

El canto de apareamiento de *A. varia* presentó una frecuencia de 425.16 ± 37.27 Hz ($387.89 - 462.43$), con una mayor intensidad entre 320 y 460 Hz, una duración promedio de 3.43 ± 0.08 seg., con una FRP de 42.16 ± 0.56 pulsos por seg. (n

= 5). La amplitud y el espacio entre pulsos fue constante desde el inicio hasta el fin (Figs. 3 y 4b).

El canto de apareamiento produjo como respuesta en las hembras de las dos especies el canto de invitación (Fig. 5). Las hembras solo hicieron el canto de invitación como respuesta al canto de apareamiento de los machos. Nunca se observó este canto con hembras solas. En el caso del canto de apareamiento siempre fue el macho quien empezaba a buscar a la hembra luego de que ésta contestara al canto de apareamiento con el canto de invitación. El macho se orientaba con el canto de invitación de la hembra hasta encontrarla; cuando los dos entraban en contacto físico, se iniciaba la cópula y terminaban los cantos. Los valores de frecuencia para este canto no se midieron dado que se registró mezclado con el canto de apareamiento de los machos.

Otros Cantos

El canto de alarma fue observado en ambos sexos para las dos especies. Lo realizaron en situaciones de estrés cuando eran manipulados para colocarlos en el montaje para realizar los registros. Esto dificultó mucho la obtención de registros confiables en las dos especies. Solo se consiguió uno para *Z. carbonaria* que presentó una frecuencia de 423.60 ± 3.11 Hz ($420.49 - 426.71$) y pulsos de 29.27 ± 0.94 ms ($28.36 - 30.21$) de duración ($n = 10$ pulsos) (Fig. 6). Para *A. varia* no fue posible realizar ningún registro de este canto de alarma.

El canto común era realizado espontáneamente tanto por hembras como por machos al caminar sobre los tallos y hojas de la planta hospedera, o cuando se alimentaba de ésta. En *Z. carbonaria* presentó una frecuencia de 322.64 ± 21.36 Hz ($301.28 - 344.00$) ($n = 10$ pulsos). En *A. varia* presentó una frecuencia de 405.33 ± 41.14 Hz ($364.19 - 446.47$) ($n = 14$ pulsos). No se observó que este canto condicionara una respuesta en otros insectos sobre la misma planta (Fig. 7).

Un canto distinto se observó cuando había dos machos de *Z. carbonaria*; éste se obtuvo dos veces durante 15 y 25 minutos continuos. Este canto consistió en pulsos de 461.50 ± 4.17 Hz ($457.33 - 455.67$) para el primero ($n = 20$ pulsos) y 472.05 ± 5.32 Hz ($466.73 - 477.37$) para el segundo. Este patrón se denominó comunicación entre machos (Fig. 8).

Diferencias Entre Especies

Al comparar los cantos de apareamiento de los machos de las dos especies, se encontraron diferencias significativas entre la frecuencia, duración del canto y la FRP (Tabla 1). Los oscilogramas

mostraron dos cantos muy distintos en su forma. El canto de apareamiento de *Z. carbonaria* mostró una serie de pulsos espaciados que van perdiendo amplitud a medida que transcurre el canto. (Fig. 2). El canto de apareamiento de *A. varia* presentó pulsos continuos con amplitud constante aminorando solo al inicio y al final del canto (Fig. 3). Las gráficas de análisis de espectro (intensidad vs frecuencia) de los cantos de las dos especies mostraron que la mayor intensidad (dB) se presenta en frecuencias diferentes para cada especie.

Discusión

Se confirmó por primera vez que en la superfamilia Cercopoidea se presenta la comunicación por vibraciones a través del sustrato (tallos y hojas de las plantas hospederas). Igual que sucede en Cicadellidae (Claridge y Howse 1968, Heady *et al.* 1986), en Cercopidae los timbales, en hembras y machos, son los que producen las vibraciones que se transmiten por el sustrato. En Delphacidae solo los machos poseen timbales funcionales; las hembras producen las vibraciones con movimientos rápidos del abdomen sin tocar el sustrato (Ichikawa 1974, 1976).

El menor tamaño de los insectos de estas familias sugiere que es más efectiva la comunicación por sólidos que por el aire. El sonido al transmitirse por el aire, un medio menos denso que los sólidos, pierde energía más rápidamente, limitando así el alcance de los cantos (Ewing 1989). Para las dos especies bajo estudio, esta forma de comunicación es importante en el comportamiento reproductivo para el reconocimiento intraespecífico y para la ubicación de la pareja para el apareamiento. Siempre fue el macho el que inicio la comunicación y búsqueda de la hembra. Esta se limita a responder los cantos del macho para orientarlo, permaneciendo inmóvil en su sitio de alimentación. Este comportamiento contrasta con el de otros homópteros como *N. lugens* (Homoptera: Delphacidae) donde la hembra es la que inicia la comunicación (Ichikawa 1974, 1976). Al ser cantos transmitidos por sólidos, los machos pueden determinar el origen y la dirección de donde provienen los cantos mas fácilmente que si el sonido fuera transmitido por el aire (Michelsen *et al.* 1982).

En algunas especies de importancia agrícola de las familias Cicadellidae y Delphacidae, se utilizaron los cantos para diferenciar especies e incluso híbridos resultantes de las mismas (Claridge y Howse 1968, Ichikawa 1974, 1976, Heady *et al.* 1986). En el caso de *Z. carbonaria* y *A. varia* las diferencias entre los cantos de apareamiento demuestran que eventualmente podría utilizarse como

herramienta taxonómica, como por ejemplo para distinguir entre especies crípticas. Al igual que Claridge y Howse (1968), Ichikawa (1974, 1976), utilizó el canto de apareamiento para realizar las comparaciones entre las dos especies. Heady *et al.* (1986) utilizaron el canto común para realizar un cladograma con 11 especies del género *Dalbulus*. En el caso de los cercópidos el canto de apareamiento es mejor que el canto común para encontrar diferencias entre especies.

Los otros patrones encontrados demuestran que estos insectos tienen un repertorio variado de cantos para diferentes situaciones. Para su correcta descripción es necesario una investigación más detallada con situaciones diferentes a las utilizadas en este estudio. En el caso de la comunicación entre dos machos, no se observó un comportamiento que pudiera arrojar alguna información útil sobre la finalidad de este canto. Siempre estuvieron quietos en su sitio de alimentación durante todo el tiempo que duró su comunicación.

Esta nueva información sobre la familia Cercopidae podría explicar algunos aspectos de su comportamiento, como parte del conocimiento básico que se debe tener de un insecto plaga. Hunt y Nault (1991) encontraron que los machos de *Graminella nigrifrons* (Forbes) (Homoptera: Cicadellidae) utilizan una estrategia llamada "call-fly" (llamar - volar) para buscar las hembras. El macho se posa sobre una hoja y llama de forma espontánea esperando la respuesta de una hembra cercana. Si no hay respuesta el macho vuela a otra planta. Con las observaciones realizadas en *Z. carbonaria* y *A. varia* se encontró un comportamiento similar por parte de los machos. Aunque ellos fueron puestos de forma manual sobre la planta, pasado un tiempo realizaban el canto de apareamiento esperando respuesta de alguna hembra. En el campo este comportamiento podría explicar porqué en algunos casos, en los muestreos realizados con pases de jama, se capturan más machos que hembras.

Conclusiones y Recomendaciones

La metodología de adquisición de los registros directamente del sustrato demostró ser fácil y confiable; no es necesario someter los insectos a espacios reducidos que limiten o afecten su comportamiento natural. Esta metodología es fácilmente adaptable para otras familias de homópteros que tengan la misma forma de comunicación a través del sustrato.

Se comprobó que los insectos de la familia Cercopidae utilizan cantos transmitidos a través del sustrato para comunicación intraespecífica. Estos cantos se producen en el timbal, el cual es funcional

tanto en machos como en hembras. Una función de este tipo de comunicación es la identificación y ubicación de pareja para el apareamiento. En *Z. carbonaria* y *A. varia* siempre fue el macho el que inició la comunicación y posterior búsqueda de la hembra.

Aunque las hembras contestaban el llamado del macho con el canto de invitación, nunca se movieron de su sitio de alimentación. Este canto de invitación es también el responsable de la orientación del macho hasta el sitio donde está situada la hembra.

Se encontraron otros patrones no relacionados directamente con el apareamiento, como el canto común, de alarma, lo que sugiere que existen otros cantos para diferentes situaciones. El canto denominado "comunicación entre machos" de *Z. carbonaria* se detectó solo entre machos. Lo realizaron independiente de la presencia o no de las hembras.

En el canto de apareamiento se encontraron diferencias significativas en términos de frecuencia, duración del canto y número de pulsos por segundo, entre las dos especies. Estas diferencias sugieren que podrían servir como herramienta taxonómica para identificación de especies.

La comunicación vibracional es un aspecto completamente nuevo para el estudio de la biología de la superfamilia Cercopoidea y abre un nuevo campo de investigación que podría explicar muchos aspectos desconocidos de la biología de este grupo de insectos. Dado que los cercópidos de importancia económica son insectos biológicamente desconocidos y difíciles de manejar, se justifica un estudio más detallado que permita caracterizar los cantos de otras especies de importancia económica para apoyar la taxonomía del grupo y comprender un poco su comportamiento en el campo.

Agradecimientos

Agradecemos al Dr. Paul-Andre Calatayud por la colaboración brindada en la parte técnica, en la revisión de este artículo y del informe de tesis. Se agradece también a Ulises Castro, Guillermo Sotelo, Anuar Morales y Reynaldo Pareja por sus ideas, críticas y apoyo constante durante el desarrollo del trabajo. Este trabajo se realizó gracias a las facilidades del Proyecto de Gramíneas y Leguminosas Tropicales, CIAT.

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Tabla 1. Diferentes parámetros evaluados (promedio $\pm$ error estándar*) a partir del canto de apareamiento registrado en los machos de *Z. carbonaria* y *A. varia*.

Parámetro	<i>Z. carbonaria</i> (n = 11)	<i>A. varia</i> (n = 5)
Frecuencia (Hz)	317.39 $\pm$ 23.25 a	425.16 $\pm$ 37.27 b
FRP (pulsos por seg.)	10.50 $\pm$ 0.37 a	42.16 $\pm$ 0.56 b
Duración del canto (seg.)	9.50 $\pm$ 0.59 b	3.43 $\pm$ 0.08 a

* Para cada parámetro valores seguidos con la misma letra no presentan diferencias estadísticas significativas según la prueba de Tukey $\alpha = 0.05$

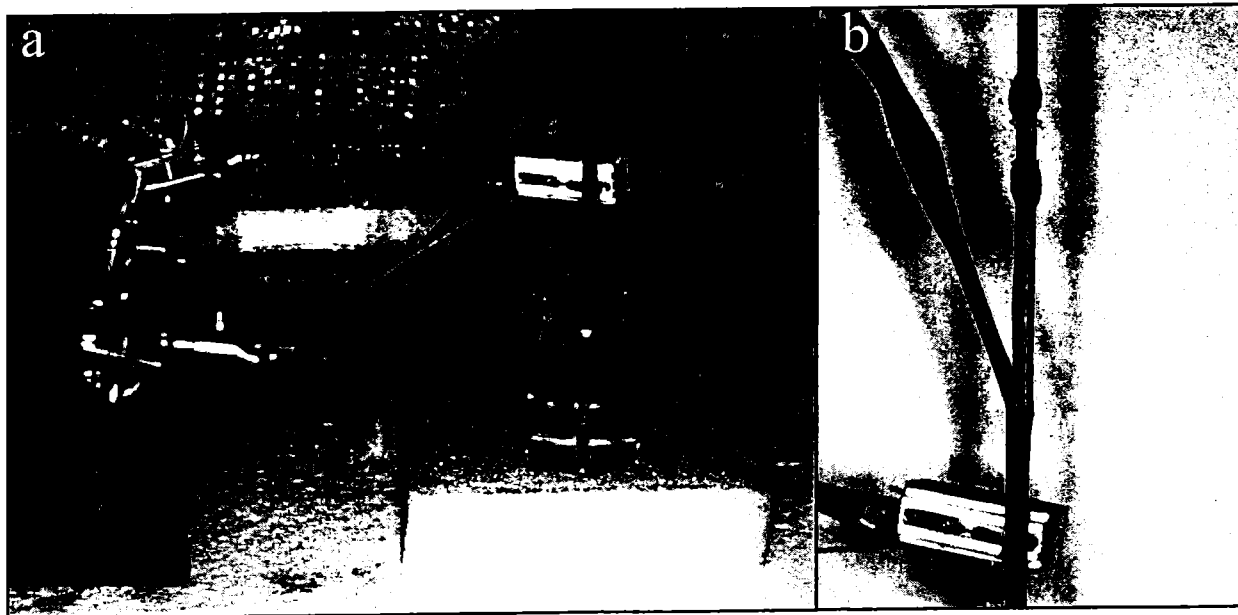


Figura 1. Montaje para la adquisición de los registros: a) plano general del montaje, b) detalle de la posición de los insectos con relación al cartucho fonográfico.

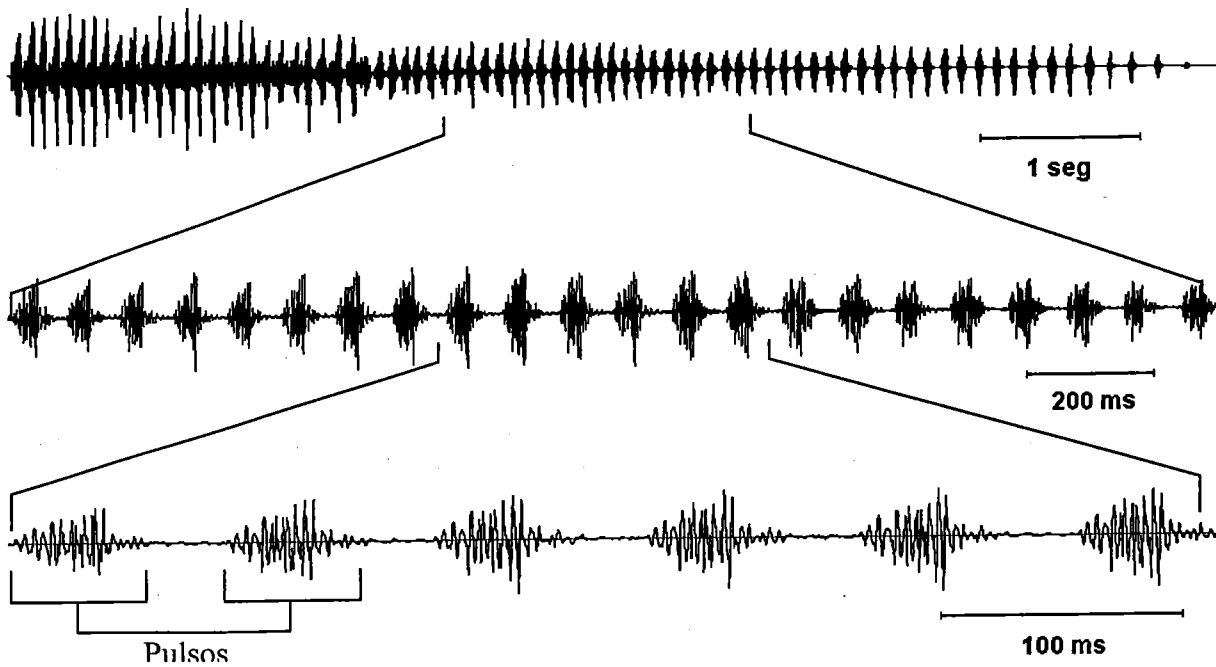


Figura 2. Oscilograma en tres escalas diferentes del canto de apareamiento o cortejo, realizado por el macho de *Z. carbonaria* para llamar a la hembra.

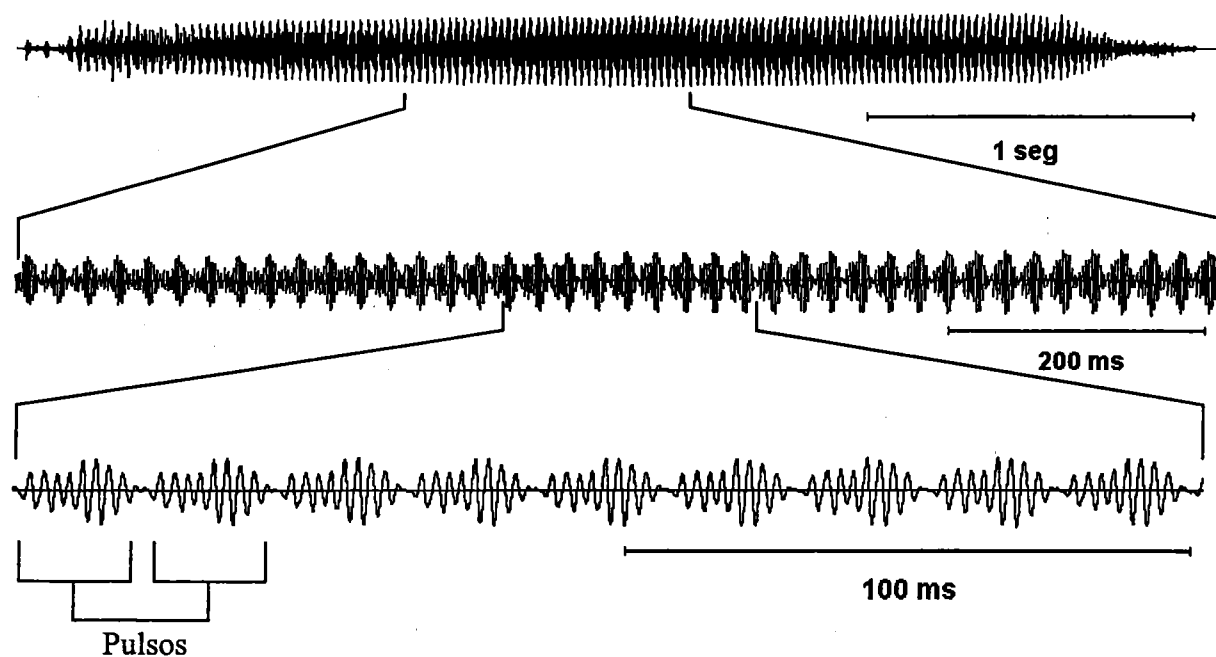


Figura 3. Oscilograma en tres escalas diferentes del canto de apareamiento o cortejo, realizado por el macho de *A. varia* para llamar a la hembra.

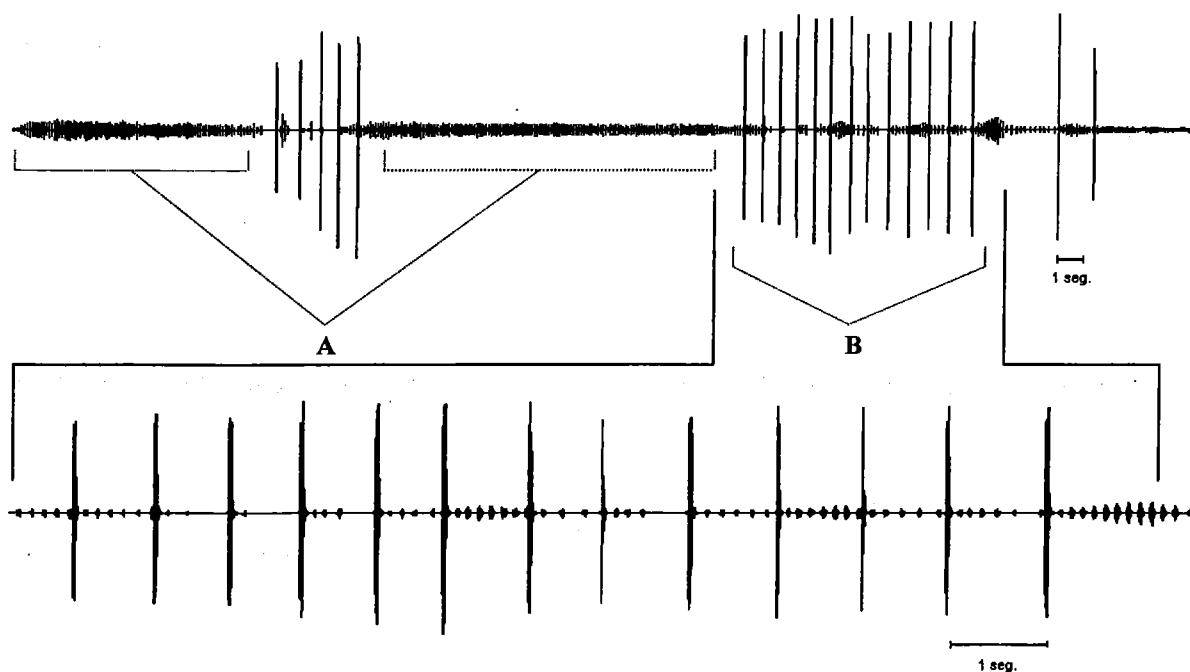


Figura 5. Oscilograma del intercambio de cantos entre un macho (canto de apareamiento A) y una hembra (canto de invitación B) de *Z. carbonaria*.

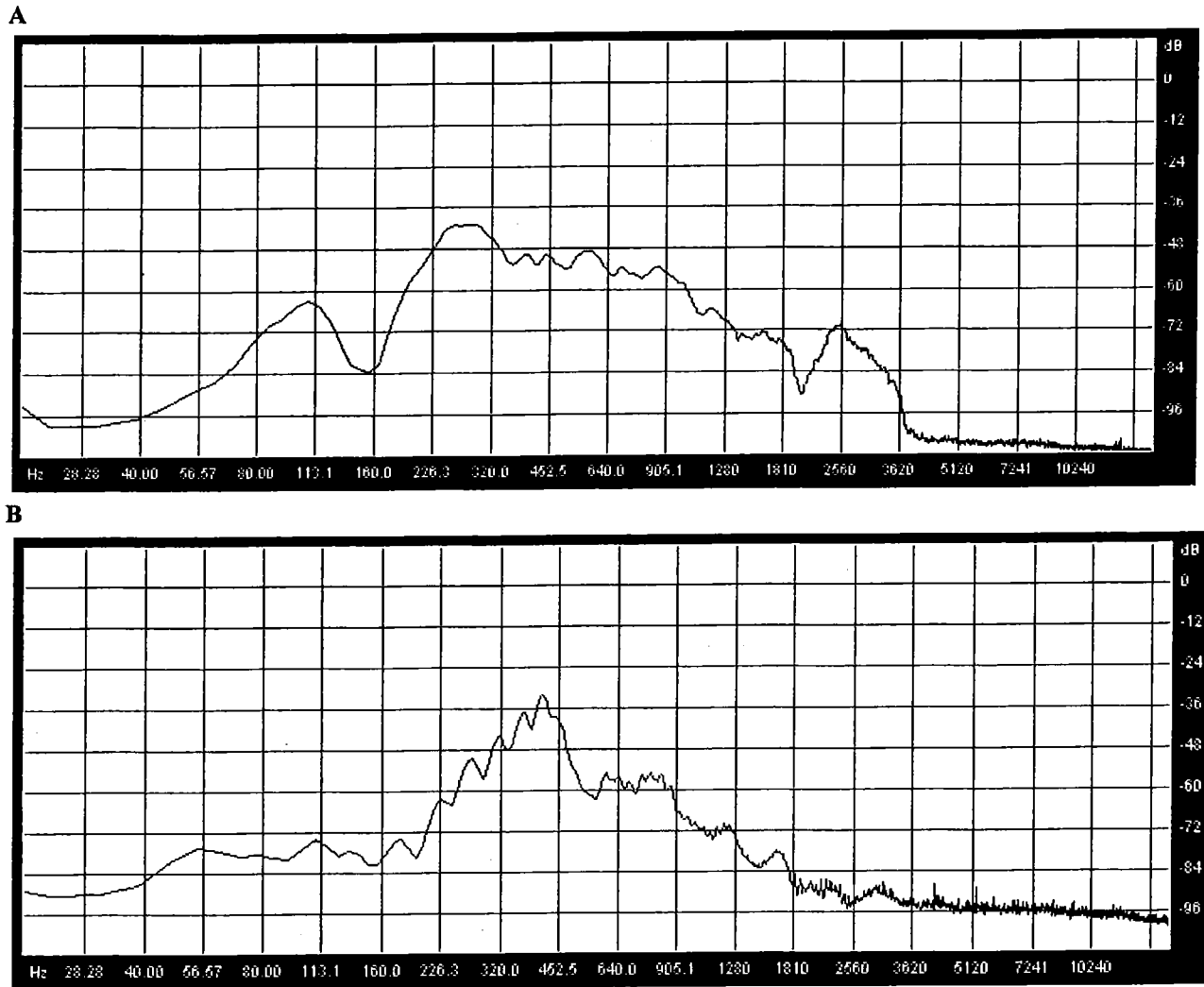


Figura 4. Análisis de espectro (frecuencia vs intensidad) del canto de apareamiento de los machos de las dos especies estudiadas. **A.** *Z. carbonaria*, la mayor intensidad se encuentra entre 220 y 330 Hz. **B.** *A. varia*, la mayor intensidad se encuentra entre 320 y 450 Hz.

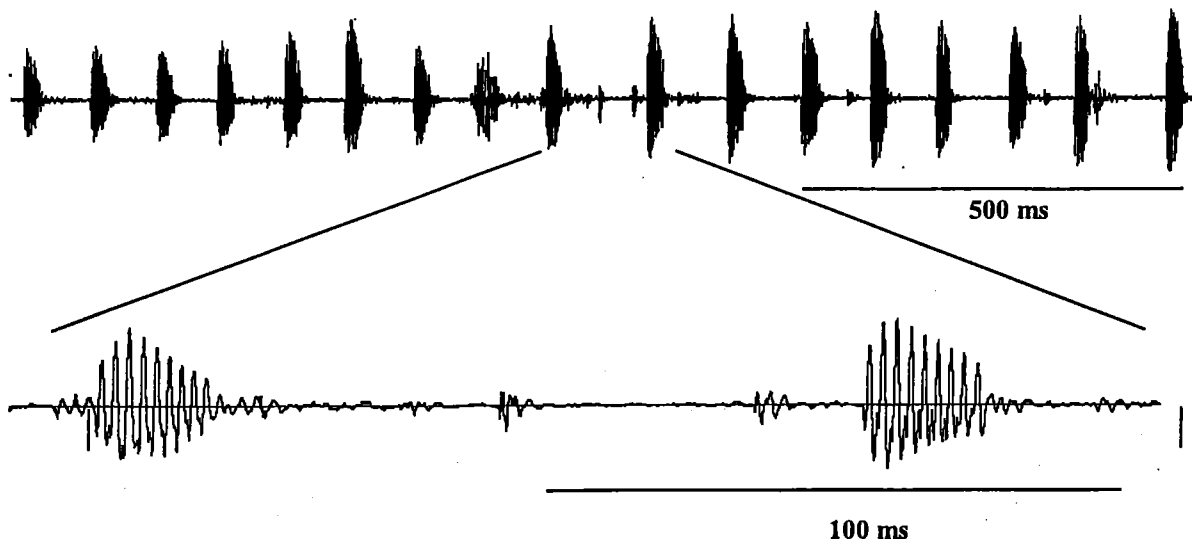


Figura 6. Oscilograma del canto de alarma de una hembra de *Z. carbonaria*.

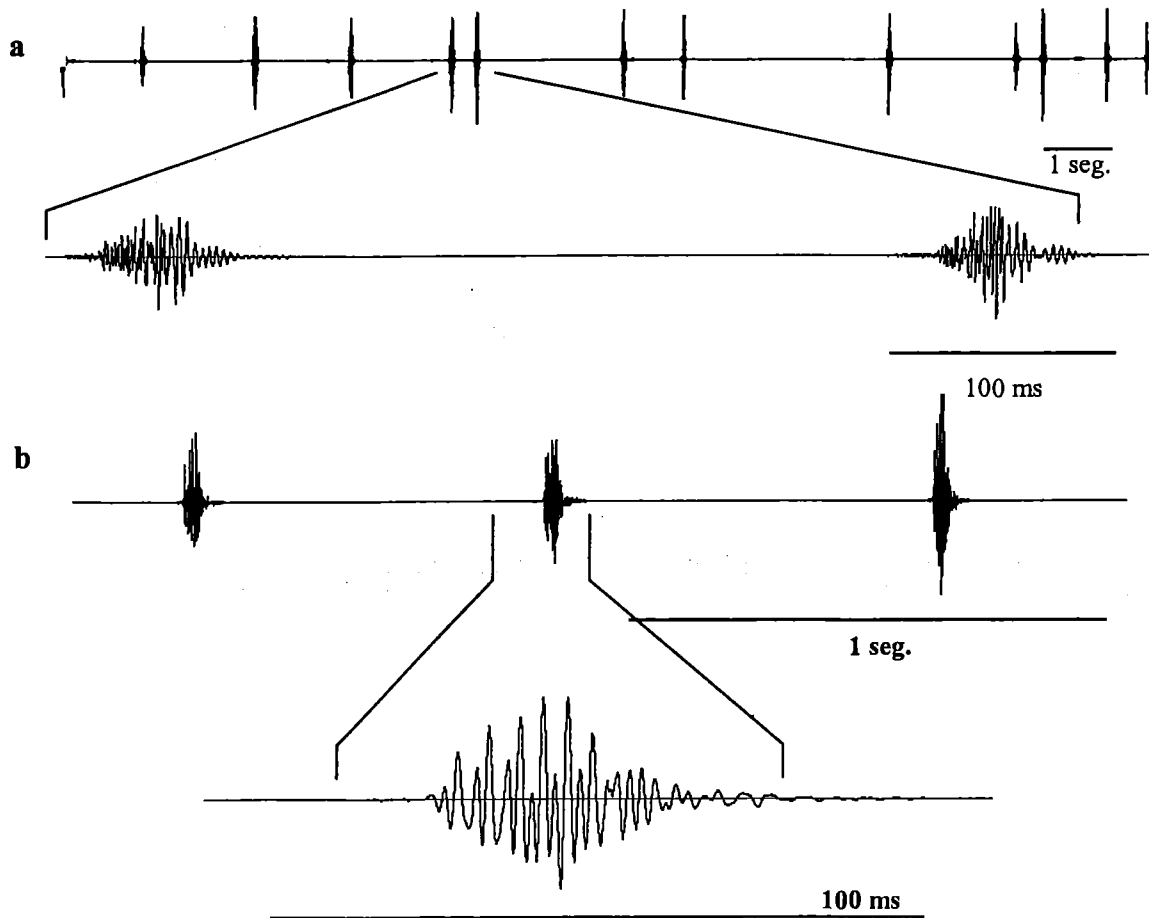


Figura 7. Oscilograma del canto común de: a) *A. varia* y b) *Z. carbonaria*.

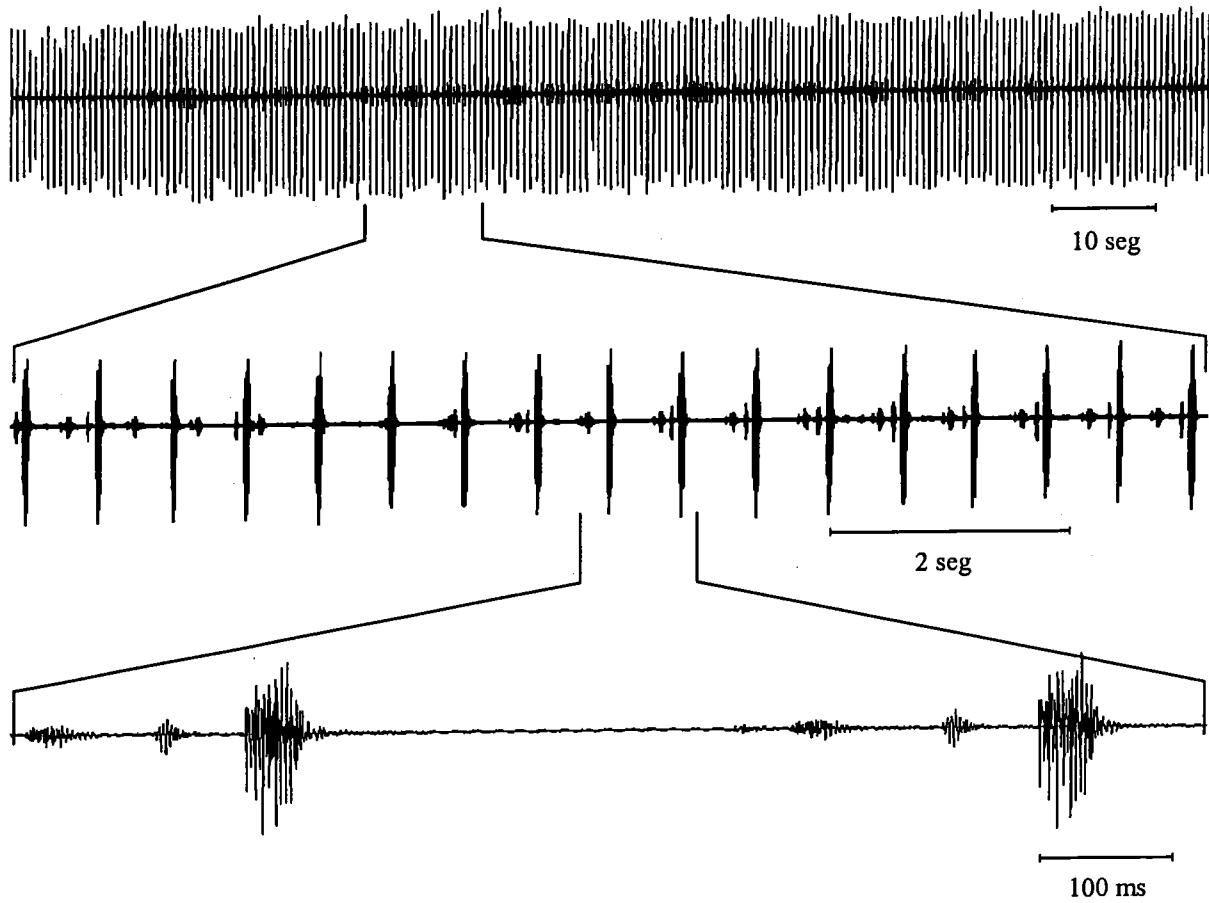


Figura 8. Oscilograma en tres escalas diferentes de la comunicación entre dos machos de *Z. carbonaria*. El de mayor amplitud corresponde al macho que estaba en el mismo tallo del cartucho; el de menor amplitud es de otro macho que estaba en un tallo adyacente. Las dos plantas tenían las hojas en contacto.

The spittlebug *Philaenus spumarius* feeds from mature xylem at the full hydraulic tension of the transpiration stream

M. MALONE¹*, R. WATSON² AND J. PRITCHARD²

¹Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK

²Department of Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK

Received 12 February 1999; accepted 23 April 1999

SUMMARY

Feeding dynamics in the spittlebug *Philaenus spumarius* were analysed to determine the food source. Evidence from previous reports indicates that this species and similar insects feed from the xylem. However, it is not clear whether they extract sap from the main transpiration stream, or from some subsidiary compartment of xylem, such as immature or cavitated vessels. In feeding from such subsidiary compartments, the insects could avoid the large hydraulic tensions thought to prevail in xylem on the main transpiration stream. *Philaenus*, for example, is shown here to initiate feeding, and to feed rapidly, from plants in which the full xylem tension is estimated at -10 bar. From measurements of feeding rates and feeding patterns in stressed and unstressed plants, it is shown that *Philaenus* cannot feed from subsidiary xylem compartments. It is concluded that this insect feeds directly from the main transpiration stream, and at the full hydraulic tension which prevails there. The anatomy of the feeding pump in *Philaenus* appears consistent with this conclusion. Spittlebugs therefore offer an experimental tool for quasi- non-invasive sampling of the transpiration stream.

Key words: *Philaenus*, xylem sap, transpiration stream, hydraulic tension, spittlebugs.

INTRODUCTION

Many insects of the cicadomorph families (Cicadidae, Cercopidae 'spittlebugs', and Cica-dellidae subfamily Cicadellinae) are believed to feed on xylem sap (Dolling, 1991). Evidence from electropenetration graphs (EPG) and other sources suggest that certain other species, such as the planthoppers *Nilaparvata lugens* (Kimmins, 1989) and *Nephotettix virescens* (Khan & Saxena, 1984), can divert their feeding to the xylem for short periods, possibly to correct imbalances in their nutritional or fluid intake (Spiller *et al.*, 1990).

Evidence for xylem feeding by insects comes from several sources:

- Microscopic examination of feeding sites of a number of cicadas and spittlebugs indicates that the stylet sheath often ends at or near a xylem vessel (Withycombe, 1926; Houston *et al.*, 1947;

Wiegert, 1964; Cheung & Marshall, 1973; Horsfield, 1978; R. F. Mizell & W. J. French, unpublished, cited in Andersen *et al.*, 1989; Crews *et al.*, 1998).

- The spittlebugs *Draeculacephala minerva* and *Neokolla circellata* (= *Hordnia circellata*) were shown to feed from xylem zones, but not phloem zones, of partially peeled grape stem (Houston *et al.*, 1947).
- Dyes which travel in the xylem may rapidly appear in the excreta of feeding spittlebugs (Houston *et al.*, 1947; Wiegert, 1964; Horsfield, 1978; Khan & Saxena, 1984).
- The putative xylem-feeding species usually have massively developed cibarial dilator muscles, with a large and heavily reinforced precibarium (Newby, 1979; Backus, 1985). These anatomical adaptations would be compatible with sucking against the strong tensions thought to occur in xylem.
- The excreta of these insects is very dilute (Cheung & Marshall, 1973) and contains little or no sugar

*Author for correspondence (tel +44 1789 470382; fax +44 1789 470552; e-mail mike.malone@hri.ac.uk).

(Withycombe, 1926; Andersen *et al.*, 1989) unlike the sugar-rich 'honeydew' excreted from phloem-feeding insects. The few solutes that are present in excreta are mostly mineral ions, including calcium, again consistent with a xylem origin (Cheung & Marshall, 1973; Andersen *et al.*, 1989).

- Spittlebugs produce large quantities of excreta (Houston *et al.*, 1947; Wiegert, 1964; Mittler, 1967; Horsfield, 1978), at rates of up to 100-fold greater than in phloem-feeding insects of comparable size. Despite these high rates of feeding *Philaenus* has a low growth rate and produces only a single generation each year in the UK (Stewart & Lees, 1996) and North America (Wiegert, 1964). This indicates that the food source must be very poor in organic compounds, again consistent with its being xylem sap.
- *Philaenus* exhibits low feeding 'efficiency' (Llewellyn, 1982), consistent with the notion that a considerable proportion of its available energy is consumed in powering the feeding pump against strong xylem tensions (Raven, 1983).

The xylem sap of transpiring plants is believed to consist of a dilute solution of mineral ions, and organic and amino acids, together with trace compounds such as ABA (Gollan *et al.*, 1992). However, this is difficult to determine accurately because pure xylem sap cannot easily be obtained from transpiring plants. The 'xylem sap' which issues from root stumps or which can be expressed from excised organs may have a solute profile different from that of undisturbed xylem sap because of contamination and dilution during excision and collection, and through alterations in the driving force, pathway, and solute-reflecting properties of the flow. Guttation fluid is also of uncertain relationship with xylem sap, and it cannot be collected during periods of rapid transpiration. It is not currently possible to extract xylem sap directly from the transpiration stream using syringes because, at the high tensions that exist there, attempts to pull water out cause cavitation.

Insects which feed from the main transpiration stream would routinely have to extract xylem fluid against large negative pressures. This would be energetically expensive and would involve flow of water under metastable conditions liable to disruption through cavitation and air-seeding. Some xylem feeders might avoid the largest sap tensions, for example, by feeding for all or part of their life cycle on underground plant parts, in which xylem tensions are smaller (Raven, 1983). Others might feed only at night when the transpiration rate and xylem tension are smaller, or they may target small plants of damp environs where transpiration rates and xylem tensions never become very large. But there are many cases in which adult, nymph, or both,

have been observed to feed for prolonged periods during the middle part of the day in temperate climates, in summer, from the shoots of tall herbs and trees (Withycombe, 1926; Mittler, 1967). According to the 'Cohesion-Tension' theory of the ascent of sap, the xylem tension in these situations would be expected to be strongly negative, perhaps -5 to -20 bars. It seems almost incredible that insects could feed against such large tensions. The largest 'suction lift' reported for a man-made device is only 17 m (Hayward, 1970) equivalent to 'pulling' water at a tension of *c.* -0.7 bar (pressure is given here in absolute units, with 0 being a perfect vacuum and +1 being atmospheric pressure). Stylets operating at high tensions would have to be devoid of air-nucleation sites on all inner surfaces and must exclude air efficiently throughout their length. At a xylem tension of -5 bar, for example, a crack of only *c.* 0.25 μm radius along the stylet or between the stylet and the xylem walls would be sufficient to admit air from the surrounding air spaces, causing embolism. Mechanical and energetic considerations raise further doubts about whether insects are physically capable of feeding against high xylem tensions (Raven, 1983). Alternative interpretations of their feeding behaviour have therefore been proposed:

- The hydraulic tension in the transpiration stream might not be as large as previously envisaged (Zimmermann *et al.*, 1994; Canny, 1998). Thus, the insects could feed from the xylem by pulling against smaller hydraulic tensions, of perhaps only +1 to -2 bar.
- The insects might feed from a compartment of xylem which does not contain the full tension of the transpiration stream. This could be achieved if: the insects deliberately cavitate xylem vessels as they push in their stylets which would immediately release the tension within the vessel, and enable the insect to mop up the sap with minimal effort (Sperry *et al.*, 1996); or, the insects might probe xylem elements which are immature and which retain a functional plasmalemma, internal solutes, and some turgor pressure. The outermost xylem regions are those most accessible to an insect's stylet. In rapidly growing dicot. stems especially, such regions will contain a significant proportion of immature vessels (Milburn, 1996), possibly with positive turgor pressures. Even if not positive, the pressure inside such cells would be elevated to some extent by their solute content, and would thus be less extreme than in neighbouring mature vessels, which convey the full transpiration stream.

These possibilities are investigated here in the spittlebug *Philaenus spumarius* using continuous monitoring of feeding rate and other techniques.

MATERIALS AND METHODS

Vicia faba L. cv. The Sutton (dwarf broad bean) was grown in peat-based compost in the glasshouse for 4–7 wk. For one experiment, plants were grown hydroponically in aerated nutrient solution. Plants were brought into the laboratory several days before the experiment. *Philaenus spumarius* L. ('meadow spittlebug') adults were collected by sweep-netting vegetation on local uncultivated land. They are common from June to October on a wide range of plants. *Philaenus* is recorded from >500 host species; more than any other insect (Thompson, 1994). Insects were brought into the laboratory and placed on *Vicia* plants.

Continuous recording of excretion

A *Vicia* plant was supported by clamp-stands so that some leaves were over the pan of an analytical balance (Sartorius RD200 (Sartorius UK, Epsom, Surrey, UK) or Mettler AT250 (Mettler UK, High Wycombe, Bucks, UK), both stable to $\pm 10 \mu\text{g}$). The balance housing was kept open to allow access of the plant. A Perspex box enclosed the balance and plant to exclude draughts. Irradiance from overhead fluorescent tubes was $75\text{--}100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) at plant height. In some experiments higher irradiance ($c. 400 \mu\text{mol m}^{-2} \text{s}^{-1}$) from a mercury vapour lamp (with 10 cm of water as a heat filter) was used. Humidity and temperature around the plant were measured with a logger (Datahog; Skye Instruments, Isle of Skye, UK) and controlled by ventilating the chamber with an air pump. One or a few *Philaenus* adults were transferred to the plant. When droplets of excreta were observed, the plant was moved so that droplets from a single adult landed in a small dish of paraffin oil on the balance pan. Readings from the balance were recorded continuously by computer, using customized software.

Only adults insects were monitored in such experiments because the nymphs create froth from their excreta rather than ejecting discrete droplets and are therefore unsuitable for measurements of feeding rates in the manner described.

Continuous measurement of leaf thickness

Leaf thickness was measured using a computerized system of transducers (ST200 Linear Variable Differential Transformers; Sangamo, Bognor Regis, W Sussex, UK) as described by Malone (1992). During each experiment, blank transducers were run, which were identical to the leaf thickness transducers, except that they contained no leaf. In one experiment, hydroponic root medium was siphoned out and replaced by similar medium containing polyethylene glycol 6000 (PEG). This

procedure took *c.* 3 min to complete. Experiments were repeated at least twice.

Xylem tension during feeding in the field

Unlike the adults, *Philaenus* nymphs do not jump, and they are therefore more convenient for work in the field. The nymphs were located by their spittle masses on a variety of host species. One leaf close to a spittle mass was enclosed in a polythene bag and shaded for *c.* 10 min. The nymph was then encouraged from its spittle mass by disturbing it with a plastic taper. Most nymphs quickly began feeding at a new site nearby. When renewed feeding was confirmed by visible excretion and the beginnings of a new spittle mass, the neighbouring bagged leaf was excised and its water potential determined using a portable pressure bomb (SKPM 1400; Skye Instruments). Weather conditions and air temperature were also recorded.

Electron microscopy

Tissue was cut from *Vicia* using a razor blade, rinsed in tap water for 30 s, and plunged into liquid N_2 . The tissue was freeze-dried overnight, shadowed with gold, and viewed under the scanning electron microscope (SEM; Cambridge Instruments, Cambridge, UK). *Philaenus* adults were also freeze-dried and shadowed with gold. Stylets were fixed in glutaraldehyde, dehydrated in ethanol, embedded in LR2 resin, and sectioned at $2 \mu\text{m}$ intervals. Xylem vessel diameters and stylet inner dimensions were measured using an optical caliper incorporated in the SEM.

RESULTS

Xylem tension of host plants in the field

Nymphs of *Philaenus* feed in the same way as adults but, rather than flicking excreta away as liquid droplets, they add surfactants and froth the mixture up to form the characteristic 'spittle' mass (Guilbeau, 1908). This may protect them from predators or from dehydration. When nymphs were disturbed they usually resumed feeding and began to produce froth again within 5 min, even under bright sunny conditions (Table 1). The xylem tension of the host plant was then estimated on a bagged leaf neighbouring the feeding site. In several cases, the balance pressure recorded at such times exceeded 10 bars (Table 1). Xylem tension can be approximated as the negative of balance pressure (ignoring the relatively small corrections for xylem sap osmotic pressure and for the difference between bomb pressure and absolute pressure). Since bagged leaves will have negligible transpiration, no correction is required for flux resistances within the leaf mesophyll. Thus, some nymphs began feeding from

Table 1. Balance pressures during resumption of feeding by *Philaenus nympha*

Species/ conditions	Time (BST) (hours)	Temp (°C)	Irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	rh (%)	Balance Pressure (bars)
<i>Artemisia</i> (mugwort)					
Bright sun	10.15	25.0	900	42	8.70
Variable: sun/shade	11.20	24.3	520	49	7.63
Overcast	13.09	15.8	310	40	6.63
Hazy/bright sun	11.35	18.0	700	41	7.82
Bright sun	13.45	27.7	1500	30	11.49
Bright sun	14.11	27.5	1400	30	10.87
Bright sun	14.37	29.3	1500	29	11.51
<i>Trifolium</i> (clover)					
Wet/shade	11.55	25.6	440	53	0.98
Overcast	12.33	24.2	490	51	3.80
Sun/overcast	12.38	15.0	500-900	45	7.78
Bright sun	11.38	23.0	1300	43	10.33
Hazy sun	12.22	32.8	600	37	5.42
Hazy sun/no wind	11.54	31.3	500	47	0.65
Hazy sun/no wind	10.57	25.4	500	49	1.21
Overcast/wet/humid	10.51	17.8	100	93	2.20
Light drizzle	11.22	19.5	150	90	1.10
Shade	10.34	16.0	90	60	5.58
<i>Rubus</i> (bramble)					
Shade	15.26	16.9	240	48	6.17
Overcast/windy	14.33	22.1	180	43	7.60
Shade	12.52	22.6	260	41	8.32
Hazy sun/bright sun	14.21	30.8	610	37	8.32
Overcast	11.53	19.9	150	88	0.39
Overcast/hazy sun	12.22	19.7	600	73	6.36
Overcast	13.37	21.9	400	68	7.33
Bright sun	15.10	38.8	1450	29	25.50
Bright sun	15.30	31.7	1600	30	13.58
<i>Anthriscus</i> (cow parsley; flower)					
Shade	13.28	24.6	160	37	4.28
Hazy sun	14.30	23.6	500	41	11.08
Shade	13.34	19.0	70	50	5.30

xylem even when the xylem tension was more negative than -10 bar.

Feeding anatomy and behaviour of *Philaenus* adults

A general description of the feeding anatomy of leafhoppers (including spittlebugs) is given in Backus (1985) and stylet structure has been described in a number of these insects (Pollard, 1972; Forbes & Raine, 1973). The feeding tube in *Philaenus* projects between the front legs (Fig. 1a) and is composed of two concentric pairs of interlocking stylets. The inner (maxillary) pair protrude beyond the outer (mandibular) pair and form a central feeding canal up to 1 mm long. The stylet bundle passes through a groove in the fleshy labium, into which it can be withdrawn when not in use. The central food canal is elliptical with dimensions of $c. 10 \times 8 \mu\text{m}$ over most of its length (Figs 1c, 2). Towards the stylet tip, the food canal tapers slightly to $c. 8 \times 7 \mu\text{m}$ (Fig. 2). The food canal emerges laterally at the tip of the inner stylets (Fig. 1b).

At their base, the stylets lead into a chamber

(cibarial pump or precibarium) on the underside of the head (Fig. 1a). The chamber houses a piston attached to large muscles in the anterior part of the head. This piston generates the insect's sucking action. Microscopic observations during feeding show that the stroke rate of the piston is typically $c. 1.7$ Hz (this can be seen on a downloadable video clip: '*Philaenus.avi*' [sic]; 9 Mb; HRI website (<http://www.hri.ac.uk>)).

Adults begin feeding by gripping the plant surface with the four anterior legs (the posterior pair are used only for jumping in *Philaenus* adults). They then press the tip of the labium vertically down against the plant surface. The stylets pierce rapidly down into the tissue from within the labial groove. Feeding and rapid excretion can begin within 3–5 min of arrival on the plant. Detailed observations of stylet movements in a spittlebug are reported in Crane (1971).

Continuous recording of excretion

While feeding, the adults periodically flick droplets of excreta from the tip of their abdomen. These

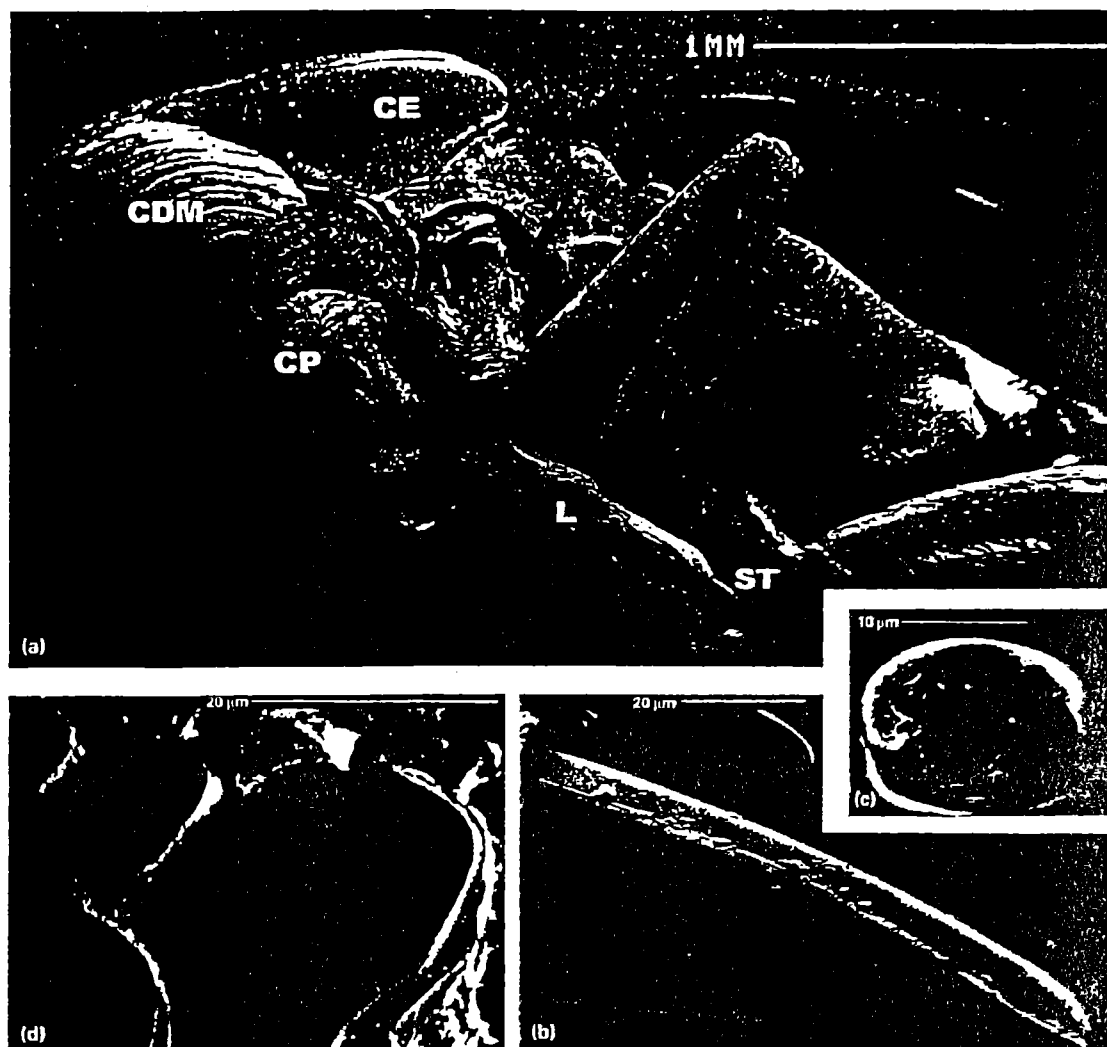


Fig. 1. Scanning electron micrographs of *Phlaenus spumarius* adult (a-c) and *Vicia* leaf section (d). (a) Ventral anterior view of *Phlaenus* adult showing cibarial dilator muscle (CDM), compound eye (CE), cibarial pump (CP), labium (L) and stylet tip (ST). Bar, 1 mm. (b) Enlarged view of stylet tip. Bar, 20 µm. (c) Transverse section from near stylet tip. Bar, 10 µm. (d) Transverse section of xylem vessels in lateral vein of *Vicia* leaf. Bar, 20 µm.

droplets are small (typically c. 0.4 mm radius or 150 nl volume) and they are ejected from the abdomen at considerable velocity. It was difficult to score these droplets reliably by eye for more than a minute or two. A computerized balance system was therefore introduced to record droplet frequency and volume over longer periods. The time of arrival of each droplet on the balance pan was identified by customized software as a transient acceleration in the trend of weight vs time (Fig. 3). The individual weight, and cumulative weight, of the droplets was also logged automatically. By flicking sub-microlitre droplets onto the balance pan from a Hamilton syringe, and by direct observation of insect excreta, it was verified that the automated system reliably

identified the timing of individual droplets. The time interval between successive droplets was typically c. 10 s in our experiments with *Vicia*.

Recordings showed that individuals often excreted for long periods (hours) with a near-constant rhythm. Fig. 4, for example, includes a period of c. 25 min of constant rapid excretion (c. 25–50 min on the x axis) during which the time interval between successive droplets never exceeded 11 s. The droplet size was also almost constant during the period. In other recordings, individuals were seen to feed for many hours from a single site, with only a few brief pauses; when pauses did occur, there was often no visible retraction of stylets.

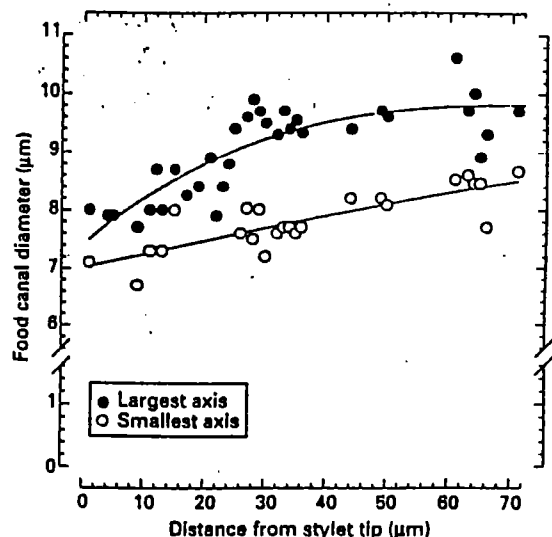


Fig. 2. Stylet food canal dimensions. Serial transverse sections were cut towards the tip of the stylet of an adult *Philaenus*. The largest and smallest diameters of the elliptical food canal were measured in each section under the scanning electron microscope. Third-order regression lines are fitted.

Effect of rapid changes in shoot water status on feeding rate

Changes in leaf water status were monitored from leaf thickness, which is closely related to leaf water status (Malone, 1992) and to xylem pressure; as leaf thickness decreases, xylem tension will become more negative. The irradiance level on *Vicia* plants was increased from c. 40 to 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using a mercury vapour lamp heat-filtered through 10 cm of water. After a lag period of a few minutes, leaf thickness showed a steep decline (Fig. 5), reflecting increased stomatal opening and water loss at the higher irradiance. Insects feeding on these same plants showed no decrease in feeding rate during or after the increase in irradiance (Fig. 5). The insects' feeding rate was similarly unaffected when shoot water status was changed rapidly by exchanging the hydroponic root medium for one containing osmoticum (Fig. 6).

Vessel dimensions

Philaenus adults fed from various sites on young

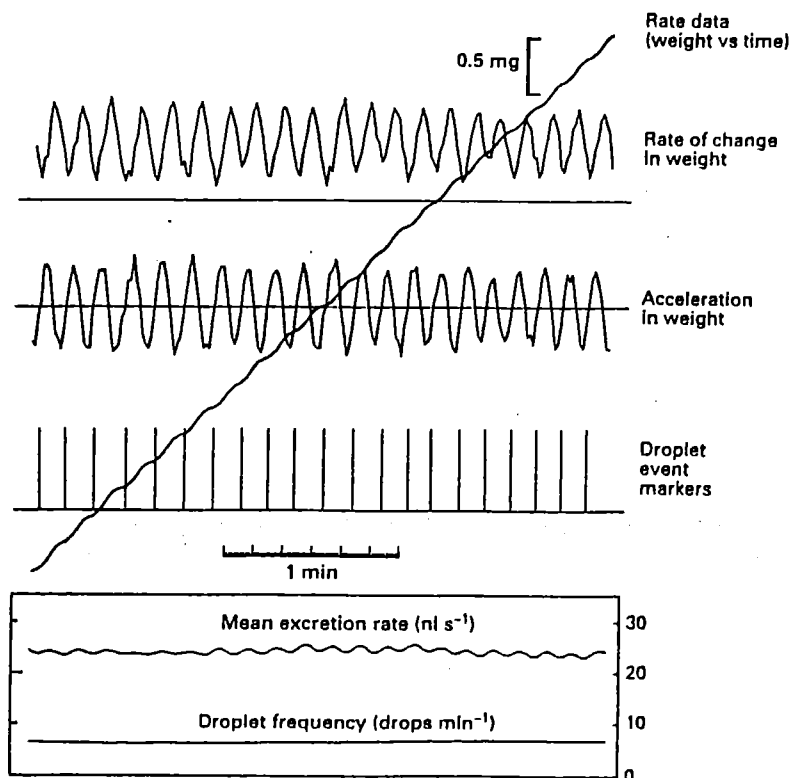


Fig. 3. Automatic recording of feeding patterns of *Philaenus*. Droplets from a feeding adult fell onto a balance pan; raw data were recorded as weight every 1 s (diagonal line). The program took the difference between successive points to give rate (top line), then acceleration, of weight with time. The program then smoothed the acceleration curve using a 3-point moving average, and identified the arrival of individual droplet 'events' as points at which the smoothed acceleration curve made a sustained transition from negative to positive. The positions of zero rate and zero acceleration are indicated by dotted horizontal lines. Mean excretion rate and droplet frequency were also calculated using a 30-point moving average (box, lower). The time marker applies to all lines, but the weight marker applies only to the line of weight vs time.

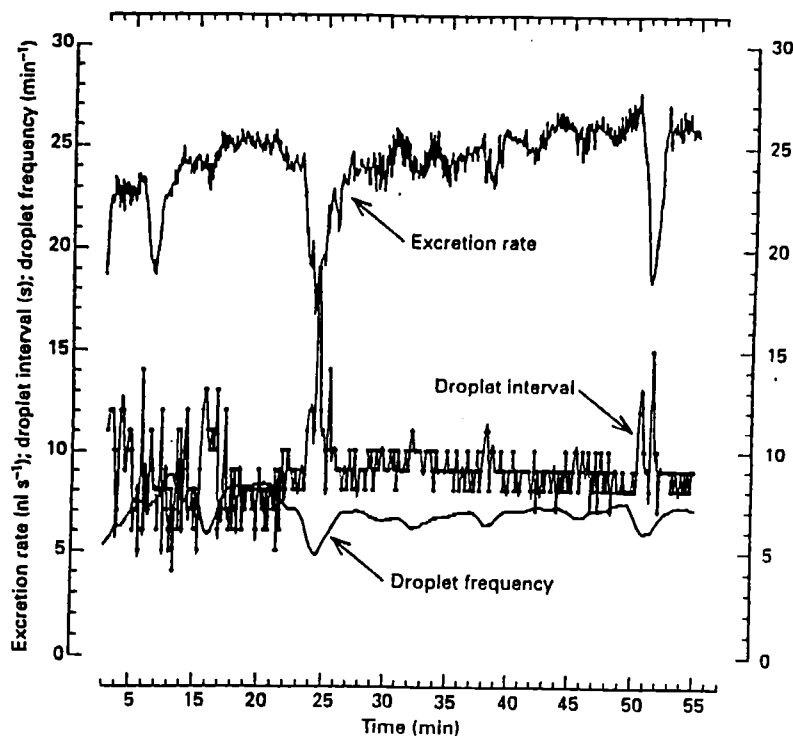


Fig. 4. Prolonged feeding of *Philaenus* without interruption. Rate of feeding and droplet excretion was recorded continuously from an adult, as in Fig. 3. A period of c. 1 h is shown. The interval (in seconds) between each successive droplet is plotted for the entire period. Mean excretion rate and mean droplet frequency are also shown.

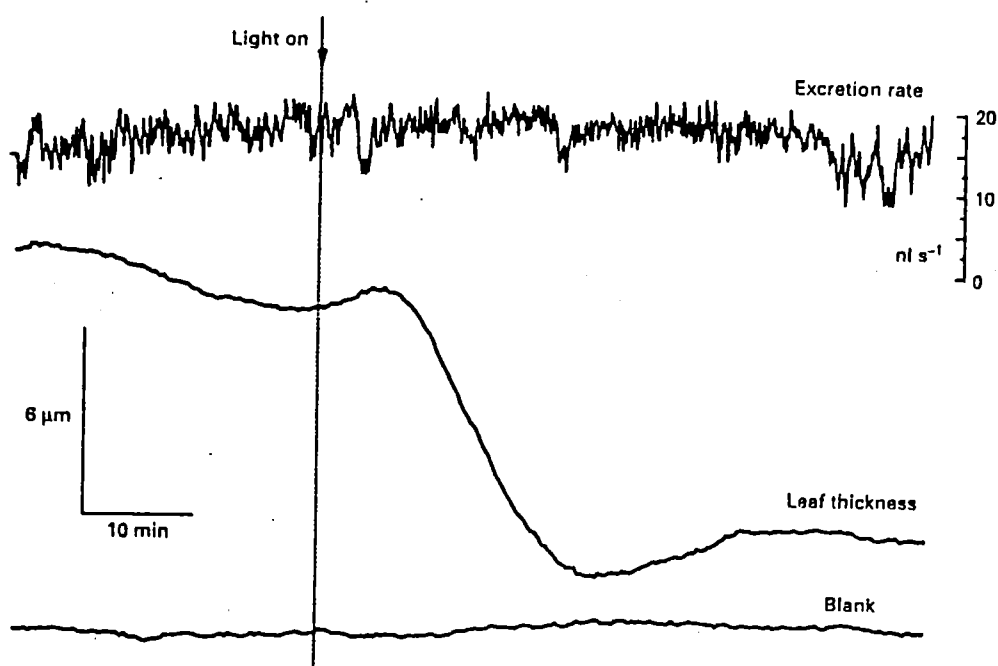


Fig. 5. Effect of increased lighting on *Vicia* leaf thickness and excretion rate of *Philaenus*. Excretion rate from a feeding adult and leaf thickness were measured simultaneously on the same plant. At the time indicated by the vertical line, a mercury lamp was switched on above the plant increasing the light intensity from 75–100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to c. 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A blank transducer was also run.

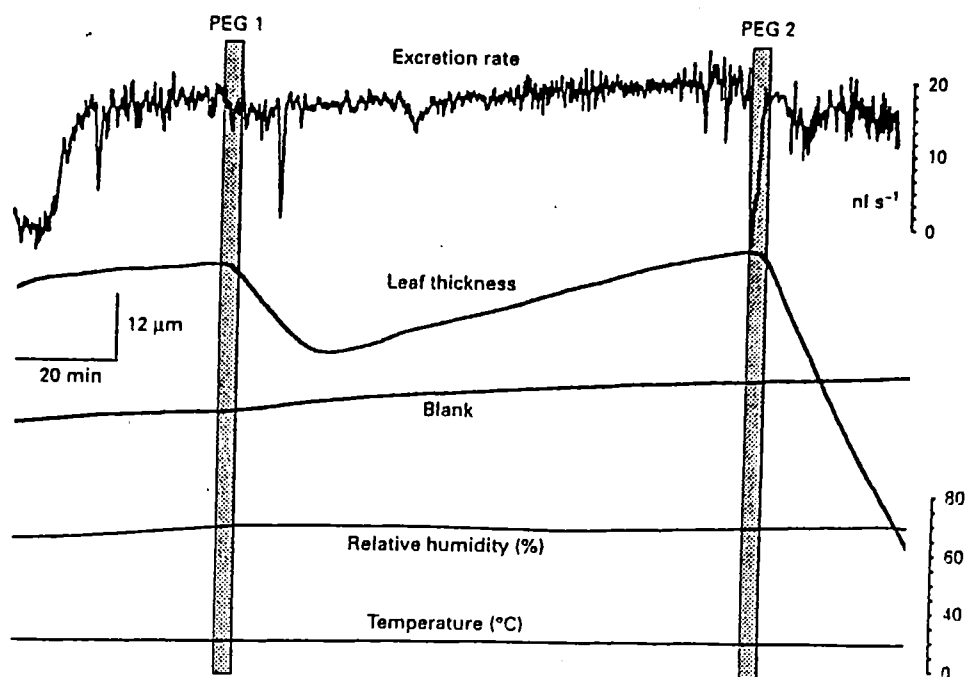


Fig. 6. Effect of polyethylene glycol 6000 (PEG) on *Vicia* leaf thickness and excretion rate of *Philaenus*. Excretion rate and leaf thickness were measured on the same plant. At the time indicated by the vertical shaded bars, the hydroponic root medium was changed to 3 bar PEG (PEG 1), and then 7 bar PEG (PEG 2). Relative humidity and temperature were measured throughout the experiment.

Vicia plants, including the stem, stipules, midvein, petiole, and laminae. One common site was over the lateral veins on the underside of leaf laminae; the xylem in such lateral veins often comprised about 4 vessels with diameters up to 17 μm (Fig. 1d).

Solute content of excreta

Excreta was collected at various times of the day and from many individual insects feeding on several different host species. Osmotic pressure was measured from melting point (Roebeling 5B; Camlab Instruments, Nuffield Rd., Cambridge, UK) and was always found to be very low. For example, the mean osmotic pressure in 15 samples collected from three tomato plants over 1 wk was 9.1 ± 2.1 mOsm (mean $\pm$ SD), with the highest individual reading being 14 mOsm or c. 0.3 bar. Most of this osmotic pressure was accounted for by mineral ions (R. Watson *et al.*, unpublished).

DISCUSSION

Philaenus excretes at extremely high rates. Values > 20 nl s^{-1} were common (Fig. 4) and we occasionally recorded sustained rates > 40 nl s^{-1} , when the insects were excreting their own body weight (c. 10 mg) c. every 4 min. The rate of excretion will approximate the rate of feeding. High rates of excretion were also found in previous studies with *Philaenus* (Horsfield, 1978) and with related insects (Mittler, 1967; Backus, 1985). Such copious production of excreta;

together with its very dilute nature (typically c. 10 mOsm in our measurements) seems consistent only with feeding from the xylem, as do various other lines of evidence summarized in the Introduction section.

Results from *Philaenus* nymphs show that rapid feeding can commence on various plants even when xylem tension exceeds -10 bar (Table 1). Furthermore, adults continued to feed rapidly from *Vicia* plants during periods when xylem tension was increased by high irradiance and by root osmoticum (Figs 5, 6). The recordings of leaf thickness, as well as tests with the pressure bomb (not shown), indicate that these treatments pushed xylem tension strongly negative (-5 to -10 bar and below). This demonstrates that *Philaenus* can feed rapidly from xylem, even in plants in which the xylem tension is strongly negative.

Three alternative possibilities by which the insects could feed from xylem but without experiencing the full tension of the transpiration stream, were listed in the Introduction section. These are discussed in turn.

Xylem tensions in transpiring plants might be much less than previously envisaged

The Cohesion-Tension theory has provided the major model of transpirational water flow for a century. It postulates the existence of continuous water columns connecting all parts of the plant with

all other parts and with water in the soil. Evaporation of water from the tops of these columns (in the substomatal cavities) generates a tension which pulls water from the soil. In extreme situations (desert plants), xylem tensions reaching -80 bars would have to be envisaged, and values of -5 to -10 bars and below would be frequent even in herbaceous plants of temperate regions (Larcher, 1980). Under these tensions, liquid water in the xylem lumina would be metastable and perhaps liable to cavitation. The Cohesion-Tension theory has had many critics (e.g. Greenidge, 1957), not least following recent work with the 'xylem pressure probe' (Zimmermann *et al.*, 1994). However, Cohesion-Tension has been defended robustly (Milburn, 1996; Sperry *et al.*, 1996; Tyree, 1997); it remains the leading theory, and is currently the only viable model. It is therefore concluded that, if *Philaenus* feeds from xylem on the main transpiration stream, it must do so against strong tensions.

Spittlebugs might feed from xylem by deliberately cavitating vessels to eliminate the negative pressure

It is conceivable that *Philaenus* stylets could cavitate xylem vessels as they penetrate. For example, the stylets might hold gas bubbles or gas nucleation sites at their tips, or they might open ventilating cracks between the stylet members or between stylet and vessel wall. On cavitation, a gas pocket of slightly above zero pressure would come into existence within the vessel, sap within the vessel would also assume a pressure of near zero, at which point it could be readily sucked out by the insect. However, it seems unlikely that the sap would remain in a cavitating vessel for long because at either side of a newly-cavitated gas pocket, the liquid water would remain continuous with water columns extending through the axial end-walls of the cavitating vessel. Water in these columns would be at the full transpiration tension. At the instant of cavitation therefore, an enormous pressure gradient will appear across the walls of the cavitating vessel, and a rapid evacuation of the vessel will ensue. The time required for such evacuation is difficult to estimate but it could be as short as a few milliseconds. Analogous water flows induced by wounding in the xylem of various plants have been measured at rates $>15-30$ mm s⁻¹ (Malone, 1996) and these involve additional resistances which would retard the flow compared with the situation at cavitation. At these rates, however, each half of a cavitating *Vicia* vessel of, for example, 10 mm in length would empty completely within 0.2 s. This allows very little time for the insect to drink.

In addition, if the insect feeds by a cavitation-and-mopping approach, it would have to tap and drain many vessels in succession to furnish sap at the observed rate of excretion. It is reported that the

stylet sheath, which marks the track of the stylets within the tissue, can be branched in *Philaenus* and other spittlebugs (Houston *et al.*, 1947; Horsfield, 1978). Thus, the insect may tap several different vessels from one penetration of the plant. However, from each cavitating vessel the insect could draw, at maximum, a volume of sap equal to the entire volume of the vessel. SEM observations show that vessels near feeding sites in the *Vicia* plants used here typically had a diameter of up to c. 17 μ m (Fig. 1d). The length of the vessels was not measured here but vessels rarely exceed 10 mm in dicot. herbs (Nobel, 1991). Thus, the volume of water contained in an individual vessel would probably be <10 mm $\times \pi(17/2)^2 \mu\text{m}^2 = 2.3 \times 10^4 \mu\text{m}^3$ or 2.3 nl, which compares with observed feeding rates of 20 nl s⁻¹ (Fig. 4) and sometimes up to 40 nl s⁻¹. Therefore, to feed by cavitation-and-mopping, the insect would have to penetrate and drain 9–17 vessels s⁻¹. Even if the vessels were much longer than estimated here, and extended the entire length of the *Vicia* plants used, their volume would be only c. 20-fold greater, and the insect would still have to tap several vessels each minute. Rapid feeding will be possible only while the insect's stylet tip is within water in a xylem vessel. If the insect has to switch to a new vessel, it would have to stop feeding, pull back its stylet tip a little, then locate, penetrate, and cavitate a new vessel. It would have to stop feeding at least transiently during this process. This is because, even if penetration and cavitation were instantaneous, secretion of a new branch of stylet canal would require some time during which the insect would be unable to feed because the stylet tip would be occluded by new sheath material. Thus, switching between vessels would necessarily involve a pause in feeding. However, recordings show that rapid feeding was frequently maintained for long periods without pause (Fig. 4). This admits no opportunity for switching between vessels.

Furthermore, *Philaenus* was observed to feed near-continuously from a single site for several hours without withdrawing its stylets. Only a limited number of vessels will be available to the stylet from a single puncture site. By contrast, during 1 h of rapid feeding by cavitation-and-mopping the insect would have to drain some 4000 vessels to account for the observed volume of excreta (assuming vessel length of 10 mm and diameter of 17 μ m, as described previously). In *Vicia* leaves, typical feeding sites contain less than a dozen vessels, and frequently there are only four vessels at feeding sites in lateral veins (Fig. 1d). Even for feeding sites on stems, there are likely to be <100 vessels within range of any one penetration site.

Therefore, on the basis of cavitation hydraulics, duration of uninterrupted feeding, and vessel volume, it is concluded that *Philaenus* cannot feed by routinely cavitating vessels. Rather, the insect must

feed from individual vessels for prolonged periods, being careful to prevent cavitation of the target vessel.

In the machaerotids, an Australian group related to spittlebugs, the nymphs are immobile and fixed to the plant. They are reported to use only a single stylet puncture, without branches, throughout each entire larval stage (Newby, 1979). Clearly, these nymphs must feed for days or weeks from a single xylem vessel, and they must avoid cavitation.

The insects might target immature vessels

With certain exceptions (St. Aubin *et al.*, 1986), xylem vessels lose their protoplast towards maturity. Thus, in growing stems there will be a zone of developing xylem, situated between the mature xylem and the cambium, in which at least some of the vessels have a protoplast, a membrane-bound vacuole with solutes and, potentially, some turgor pressure. If *Philaenus* targets such vessels, it could access fluid at a pressure substantially above that of the main transpiration stream.

Feeding from an immature vessel would cause dilution of the cell's solutes, as water enters the cell to replace that drained into the stylet. Such dilution will proceed exponentially until, by the time fluid amounting to 230% of the initial cell volume has been sucked out, <10% of the initial solutes will remain. At the feeding rate and vessel dimensions used previously (20 nl s⁻¹ and 10 mm × 17 µm diameter) this degree of dilution would be reached within 0.1 s. The turgor pressure of the cell must decline in advance of the dilution of its solutes, which means that within the first 0.1 s of feeding, the internal pressure of the immature vessel would drop to a level not significantly higher than that of the main transpiration stream. Thus, any pressure advantage afforded by the immature vessel would be extremely short-lived.

In addition, the refilling of the immature vessel, as its contents are sucked out, would be retarded by the hydraulic resistance of the plasma membrane. Hydraulic conductivity of plant membranes is typically c. 10⁻⁷ m s⁻¹ bar⁻¹ (Tomos, 1988). The surface area of membrane can be approximated as the surface area of the cell. Assuming the same vessel dimensions already used, this will be c. 534 × 10⁵ µm² or 5.34 × 10⁻⁷ m². The pressure gradient required to maintain water influx across this membrane at a typical rate of feeding (20 nl s⁻¹) would therefore be c. 200 bar. Clearly, unless the immature vessels have very unusual membrane properties, insects could not feed from them at the observed rate.

Also, *Philaenus* adults in our laboratory have been observed to feed rapidly from mature leaves and ligules of various dicots, and from the laminae of leaves of barley and other monocot. plants. Unlike growing dicot. stems, these tissues will have few, if

Table 2. Comparison of components of pump dynamics in two species of bug

	<i>Rhodnius</i>	<i>Philaenus</i>
Maximum intrinsic muscle tension (bar)	6	6
Pump stroke frequency (Hz)	3	1.7
Muscle contraction rate (muscle lengths s ⁻¹)	1	0.5
Ratio of muscle:piston area	2.5	10
Maximum pump tension (bar)	-3	-24

Data on *Rhodnius* is from Bennet-Clark (1963).

any, immature vessels. Therefore, it is concluded that *Philaenus* cannot feed by targetting immature vessels.

By elimination, therefore, we conclude that *Philaenus* must feed on xylem sap from mature vessels in the main transpiration stream, and at the full negative pressure which prevails there (to at least -10 bar; Table 1). This conclusion differs from that of Raven (1983), who argued from anatomical considerations that the insect would not be capable of feeding against tensions more negative than c. -3 bar. Raven's argument used measurements from *Rhodnius*, a blood-sucking bug (Bennet-Clark, 1963). Comparable measurements on *Philaenus*, however, indicate that the latter should be substantially more powerful (Table 2). The maximum internal tension that any muscle can generate under isometric (stationary) conditions is c. 6 bar. However, the faster the muscle contracts, the lower the proportion of this maximum that can be realized. In addition, the tension that the pump can exert on a piston will be amplified according to the ratio of the muscle's cross-sectional area to that of the piston. In *Philaenus* the muscle area is much larger than the piston area (Table 2). Also, the dilator muscle in *Philaenus* contracts more slowly than that of *Rhodnius* and is thus able to generate greater intrinsic tension. Taking these two factors into account, the suction force developed by the *Philaenus* pump should be some eight-fold greater than that of *Rhodnius*, or c. -24 bar. Some of the force generated by the pump will be dissipated in driving fluid through the stylet canal. Assuming food canal dimensions of 9 × 7 µm (Figs 1c, 2) and length of 1 mm (Fig. 1a), the Hagen-Poiseuille relationship for elliptical tubes (Nobel, 1991) indicates that feeding rates typical of those found here (20 nl s⁻¹) would require a pressure gradient along the stylet of c. 2 bar. This means that *Philaenus* should be capable of feeding on xylem sap at tensions down to c. -20 bar. This will include most plants and situations, at least over the range found in the UK.

As stated in Introduction section, insects such as *Nilaparvata lugens* are suggested to be facultative xylem feeders (Kimmins, 1989). However, from the

arguments here, it seems unlikely that such insects could feed, even briefly, from the main transpiration stream because they lack the anatomical adaptations seen in *Philaenus* and similar insects (i.e. large-bore stylet, heavily reinforced precibarium, and large cibarial dilator muscles). It is possible that the facultative feeders, with their much slower feeding rates, target immature xylem.

Despite the central importance of xylem in plant transport, there is currently no unequivocal method for obtaining pure xylem sap for analysis. However, if, as concluded here, *Philaenus* does feed directly from the transpiration stream, its excreta should contain indigestible material (i.e. calcium and other minerals) at the same concentration as present in the transpiration stream. These minerals can be assayed in small volumes of excreta using Ion Chromatography (R. Watson *et al.*, unpublished). Thus *Philaenus* (and possibly similar insects; Andersen *et al.*, 1989) offers an approach for non-destructive and quasi-continuous sampling of material in transit in the transpiration stream.

ACKNOWLEDGEMENTS

The authors are grateful to Ms C. Evered and Mr C. Clay of HRI's electron microscopy unit for preparation and sectioning of material, and to Dr D. Lees of UCNW Cardiff for help and advice. This work was funded by BBSRC.

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Egg Diapause and Pest Management of *Aeneolamia varia* (Homoptera: Cercopidae) in Venezuela

JOSE MORALES

Department of Entomology and Zoology, Universidad Centro Occidental "Lisandro Alvarado," Apartado 400, Barquisimeto, Venezuela

Environ. Entomol. 22(5): 1092-1095 (1993)

ABSTRACT Egg diapause and response of the froghopper *Aeneolamia varia* (F.) to dry conditions were studied in the laboratory. Eggs were obtained from adult females collected in the field in each of four *A. varia* generations. Three discrete groups of eggs were found: nondiapause, short-time diapause, and prolonged diapause eggs with an average time of development of 15.5, 79.2, and 196.2 d, respectively. In generation 1, nondiapause eggs accounted for 76.0% of the hatch, but in generation 2, only 13.3%. Prolonged and short-time diapause eggs predominated in generations 3 and 4, constituting 76.7 and 72.0%, respectively. Most of the eggs produced by adult females of generations 2-4 strongly resisted dry conditions. In the field, most of the *A. varia* eggs were killed by natural enemies or high temperatures (or both) at the soil surface, and only a few survived to hatch between 15 and 123 d. The predominance of nondiapause eggs early in the rainy season allows for a rapid increase in population. Most short-time and prolonged diapause eggs are laid later. This suggests that for control of this pest in sugar cane, insecticide sprays should be applied from the time of the appearance of the first population of nymphs until the development of those that give rise to adults of the generation 2.

KEY WORDS *Aeneolamia varia*, egg diapause, pest management

THE FROGHOPPER *Aeneolamia varia* (F.) is an indigenous American insect broadly distributed through the Neotropics in areas where the forest was the original vegetation (Myers 1932). In land now under cultivation or in pasture, the insect exploits numerous grasses as hosts. Nymphs and adults feed on vascular fluids of these grasses and inject damaging toxins into the roots and leaves (Urich 1913). In Venezuela, significant losses to sugar cane production commonly result (Ferrer et al. 1973).

Three or four froghopper generations are produced annually on sugar cane before the onset of the dry season. Guagliumi (1962) indicated that *A. varia* adult females mate immediately after emergence and live for ≈ 20 d, during which they oviposit up to 150 eggs. He also indicated that eggs are placed on decaying plant parts or in fissures in the soil and hatch from 13 d to several months later, depending on the presence or absence of diapause.

Diapause, an important component of insect phenology, enables many insects to synchronize their life cycles with the environment when conditions are unfavorable (Tauber et al. 1986). Photoperiod, drought, and soil moisture are factors important in the induction and duration of froghopper diapause (Urich & Pickles 1930, 1931; Evans 1971; Vreugdenhil 1984). Related studies of other insect pests have pointed out that knowl-

edge of insect egg diapause permits the development of strategies for their control (Krysan et al. 1986, Levine et al. 1992, Steffey et al. 1992).

Control of the froghopper has been achieved using insecticides (Fewkes 1969, Evans 1971, Norton & Evans 1974), but the use of natural enemies has generally proven unsuccessful (Fewkes 1967, Bennett 1984). Nevertheless, increasing commercial and environmental costs associated with insecticide control have continued to spur interest in developing a more integrated pest management program. This requires an a priori fundamental understanding of the life history of *A. varia* and the influence of environmental conditions on the development of its populations.

In an effort to clarify the life history and ecological relationships of this pest, my study was focused on the kind of diapause of eggs laid by each *A. varia* generation, the hatching times needed for each kind of egg, and the mortality of eggs exposed to dry conditions.

Materials and Methods

Laboratory Studies. Male and female adult froghoppers were collected in sugar cane fields at Patio Grande Farm near Cabudare, Lara State, Venezuela, during the rainy season of 1988. Dates of collection of generations 1, 2, 3, and 4

were 19 July, 1 September, 18 October, and 5 December, respectively. The presence of generation 1 was detected by weekly sampling after the first strong seasonal rain, whereas the collection dates and presence of the remaining generations were calculated based on known life cycle periods as well as their detection in the field (Guagliumi 1962). From 100 to 200 frog hopper adults were placed into 30-cm³ wooden box cages fitted with lateral mesh windows and a mesh lid. Cages were disinfected with 10% sodium hypochlorite (Clorox, Oakland, CA) and kept in a room at $27 \pm 2^\circ\text{C}$, $90 \pm 10\%$ RH, and a photoperiod of 12:12 (L:D) h. The bottom of each cage was provided with a plastic tray covered with paper toweling and filter paper. A sugar cane bouquet and distilled water was added daily to encourage oviposition.

Under magnification, strips of filter paper were cut so they each contained 10 frog hopper eggs. Three of these strips with 10 eggs each were placed on paper toweling in a petri dish previously disinfected with 10% Clorox. Five petri dishes were established in this manner and five treatments were done. In the first treatment, eggs were subjected to moisture immediately after collection. In the second to fifth treatments, eggs were kept in aerated jars for 1, 2, 4, and 8 mo, respectively, before application of moisture. Five replications were run. The environmental conditions were the same as described above.

Petri dishes were observed daily under magnification, and the numbers of hatched and dead eggs were recorded. For treatment 1 (eggs moistened immediately), the average number of days for hatching was computed directly in each of the four *A. varia* generations. This made possible the identification of the different types of eggs grouped into diapause categories. Dead eggs obtained in each of the four *A. varia* generations were expressed as percentages to show the influence of time of storage on egg mortality.

Statistical analyses were done using Statview 512+ statistical software (Feldman et al. 1986). Egg type data and effect of the treatments on egg mortality were tested by analysis of variance (ANOVA) using Fisher's protected least significant differences test (LSD) for mean comparisons at $P < 0.05$.

Field Studies. Field trials were performed to establish degree of concordance with laboratory findings. Eggs obtained in the laboratory (as previously described) were used. For generations 1–4, fifteen strips of filter paper each with 10 eggs were taken to the field the same day they were oviposited and pinned at random to the basal part of a sugar cane stem.

The paper strips were observed daily under magnification, and the number of hatched eggs and dead eggs were recorded. Data were expressed as percentages to determine hatch of

eggs laid directly on the soil surface by adult females.

Results and Discussion

Laboratory Studies. Eclosion periods of first-generation eggs revealed three discrete groups: nondiapaue eggs that hatched between 14 and 19 d, short-time diapause eggs that hatched between 49 and 115 d, and prolonged diapause eggs that hatched between 184 and 252 d (Fig. 1a). This pattern was repeated in the second and third generations (Figs. 1 b and c). The fourth generation did not continue this trend for reasons explained below (Fig. 1d).

Generation 1 produced a high proportion of nondiapaue eggs (76.0% of the generation hatch) and progressively fewer numbers of short-time diapause (5.3%) and prolonged diapause (4.0%) eggs (Fig. 2). This pattern became dramatically reversed in later generations. Generation 2 produced fewer nondiapaue eggs (19.3% of those hatched), but the number of short-time and prolonged diapause eggs increased to 24.7 and 46.7%, respectively. Generation 3 produced a high proportion of prolonged diapause eggs (76.7% of the generation hatch) and progressively fewer short-time diapause (6.7%) and nondiapaue (1.3%) eggs. Generation 4 produced a high proportion of short-time diapause eggs (72.0% of those hatched), and fewer nondiapaue and prolonged diapause eggs (2.0 and 10.0%, respectively).

No clear groupings were apparent in generation 4. This may have been caused by late-season environmental influences such as decreased adult feeding, low relative humidity of the soil surface, or (less likely in Venezuela) changes in photoperiod that affect formation of eggs (Urich & Pickles 1930, 1931; Fewkes 1964; Evans 1971). Undoubtedly, however, adult females classified as "fourth generation" in this study included numerous individuals that actually developed from the short-time and prolonged-diapause eggs of the earliest generations. This apparently obscured the hatch groupings established in generations 1–3.

Excluding generation 4, the average times required for development were 15.5 ± 0.09 , 79.2 ± 2.95 , and 196.2 ± 2.03 d (mean $\pm$ SE) for the nondiapaue, short-time diapause, and prolonged diapause eggs, respectively.

Mortality of *A. varia* eggs was greatly increased with delays in application of moisture (Table 1). In those eggs moistened the same day of their oviposition, the intrinsic mortality was low: 14.7, 9.3, 15.3, and 16.0% for generations 1, 2, 3, and 4, respectively. However, in similar samples of eggs stored without application of moisture for 4 mo, mortality increased greatly to 90.7, 34.0, 52.7, and 59.3% for generations 1–4, respectively. After 8 mo, almost all eggs had died.

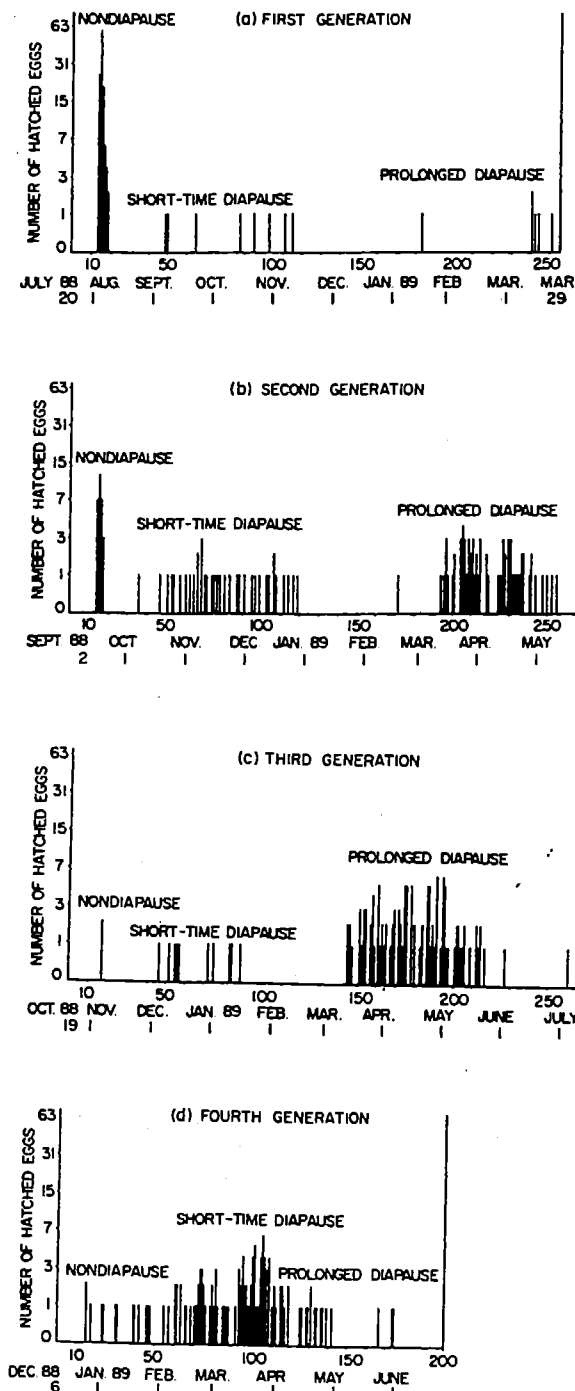


Fig. 1. Time of hatching of generations 1-4 of *A. varia* eggs.

The higher mortality recorded for first-generation eggs with delayed wetting is attributable to the higher proportion of nondiapause eggs produced by generation 1. Nondiapause eggs are evidently the least resistant to drought condi-

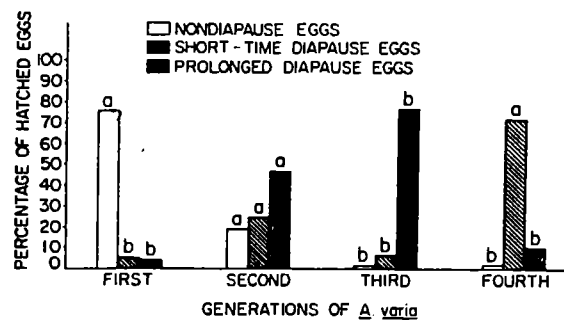


Fig. 2. Percentage of eggs hatched during each generation of *A. varia*. Bars with the same letters within generations indicate that values are not significantly different ($P < 0.05$; Fisher's protected LSD test [Feldman et al. 1986]). Results of ANOVA ($df = 2, 8$): generation 1, $F = 344.4$, $P < 0.0001$; generation 2, $F = 2.6$, $P < 0.13$; generation 3, $F = 279.0$, $P < 0.0001$; generation 4, $F = 76.8$, $P < 0.0001$.

tions. In contrast, the greater proportion of short-time diapauses and prolonged diapauses eggs laid by later adult generations contributed to the greater viability of their eggs under simulated drought conditions.

Field Studies. Measured temperatures up to 38.8°C on the soil surface, or natural enemies (mainly ants), strongly affected *A. varia* egg survival (Table 2). The largest hatch (32%) resulted from eggs laid by adult females of generation 1 at the beginning of the wet season. Most of these eggs hatched between 15 and 33 d; only one hatched at 123 d. Mortality of eggs of later generations attained 98.7% because the long incubation period of short-time and prolonged diapauses eggs permitted natural enemies or high temperatures on the soil surface to inflict that high mortality. In nature, eggs are obviously more protected in soil fissures and live through to the next year (Guagliumi 1962).

In conclusion, the ability of *A. varia* to survive year after year in sugar cane fields depends basically on the short-time and prolonged diapauses

Table 1. Influence of time on mortality of stored eggs from generations of adults of *A. varia*.

Generation	Time stored, mo ^a				
	0	1	2	4	8
% Mortality					
1	14.7d	69.3c	87.3b	90.7ab	100.0a
2	9.3d	42.6c	31.3b	34.0b	98.6a
3	15.3d	10.7d	23.3c	52.7b	100.0a
4	16.0c	23.3c	24.7c	59.3b	100.0a

Percentages followed by same letters within rows are not significantly different ($P < 0.05$; Fisher's protected LSD test [Feldman et al. 1986]). Results of ANOVA ($df = 4, 16$): generation 1, $F = 47.3$, $P < 0.0001$; generation 2, $F = 96.4$, $P < 0.0001$; generation 3, $F = 98.9$, $P < 0.0001$; generation 4, $F = 104.3$, $P < 0.0001$.

^a Based on a sample of 150 eggs per generation.

Table 2. Survival and mortality of *A. varia* eggs in the field, Patio Grande, 1988

Generations	Hatched eggs		Nonhatched eggs	
	Number ^a	Percentage	Number	Percentage
1	48 (15-30)	32.0	102	68.0
2	15 (21-123)	10.0	135	90.0
3	2 (32-33)	1.3	148	98.7
4	3 (32-33)	2.0	147	98.0

Based on 150 eggs per generation.

^a Values in parentheses indicate range of days of eclosion.

eggs laid by generations 2-4. These eggs resist the dry season. In contrast, nondiapauses eggs produced early in the wet season allow for rapid population increases. This is the natural history of a species synchronized with the climatic conditions typical of much of northern Venezuela.

Based on these data, if second-generation *A. varia* escapes insecticidal control, the greater quantity of short-time and prolonged diapause eggs produced by generations 2-4 should maintain an insect population in excess of an economic injury level. On the other hand, *A. varia* should be vulnerable to insecticides from the initial appearance of generation 1 of nymphs until the development of those nymphs that give rise to second-generation adults because nondiapauses eggs predominate at that time. Further insecticide applications then should not be necessary. Also, natural enemies that develop during this later period could possibly maintain effective control of this insect pest for the rest of the year.

Acknowledgment

I thank Miguel Rábago (Departamento de Biología, Universidad Pedagógica Experimental Libertador, Barquisimeto, Venezuela) for technical assistance during this investigation; Arthur A. Hower, Jr. (Department of Entomology, The Pennsylvania State University, University Park, State College), Robert Smith (Departamento Agrobiológico, Universidad Centro Occidental Lisandro Alvarado, Barquisimeto, Venezuela), and Charles Burandt (Biology Department, Texas A&I University, Kingsville, TX) for critical reviews of the manuscript; and Alvaro Chávez, and Franklin Gutiérrez (Departamento de Entomología, Universidad Centro Occidental Lisandro Alvarado, Barquisimeto, Venezuela) for helpful suggestions. Franklin Martínez and Antonio Escalona (Departamento de Entomología, Universidad Centro Occidental Lisandro Alvarado, Barquisimeto, Venezuela), assisted in field data collection; and the local assistants Vicente Terrón Vega, Efraín Lobatón, Antonio Pérez, José A. Taibo, and Eugenio Graterol assisted in various aspects of the field work.

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Received for publication 16 October 1992; accepted 10 May 1993.

CICLO BIOLOGICO Y COMPORTAMIENTO DEL *Salpingogaster nigra* SCHINER, PREDATOR DEL "MION" Y "SALIVITA" DE LOS PASTOS

Pedro José Pérez*
Germán Alonso Torres M.*
Jaime A. Jiménez G.**
Jesús E. Luque Z.***

RESUMEN

El ciclo de vida de *Salpingogaster nigra* Schiner (Diptera: Syrphidae), un enemigo natural del mion y salivita de los pastos *Aeneolamia varia* (F.) y *Zulia pubescens* (F.), fue estudiado bajo condiciones de campo y laboratorio en la finca "San José" en Medina (Cund.) y en el Centro Regional de Investigaciones "La Libertad" en Villavicencio. El ciclo de vida tuvo una duración de 27,37 días, discriminados así: huevo 2,7 días, larva 9,7 días según lo calculado, pupa 9,67 días y adulto 5,3 días en promedio. Con base en estudios morfológicos se determinó que la larva pasa por tres instares. La larva consume entre 14 y 20 ninfas de la plaga. En el estudio se da la descripción de los diferentes estados y se presentan observaciones sobre su comportamiento.

SUMMARY

The life cycle of *Salpingogaster nigra* Schiner, a natural enemy of the froghoppers *Aeneolamia varia* (F.) y *Zulia pubescens* (F.), was studied under field and laboratory conditions at the farm "San José" in Medina (Cund.) and at the Centro Regional de Investigaciones "La Libertad" in Villavicencio. The life cycle lasted in total 27.37 days, divided in: egg 2.7 days, calculated for the larva 9.7 days, pupa 9.67 days, and an average of 5.3 days for the adult. Based on morphometric studies it was determined that the larva has three instars. The larva consumes between 14 and 20 nymphs of the pest. The description of the stages and some behavioral observations are presented.

INTRODUCCION

De las gramíneas forrajeras introducidas a Colombia, el pasto *Brachiaria*, *Brachiaria decumbens* Stapf., ha sido la más difundida y la de mejor aceptación en regiones ganaderas del país, principalmente en los Llanos Orientales, por su buena adaptación a suelos ácidos, pobres en nutrientes (Spain, 1980) y por el incremento en la productividad por hectárea, comparado con especies nativas (Alarcón, 1980; Hutton, 1980). Sin embargo, presenta la desventaja de ser

gravemente afectado por cercópidos, como el *Aeneolamia varia* F. y *Zulia pubescens* (F.), considerados como el principal limitante fitosanitario en explotaciones ganaderas (Araújo, 1975; ICA, 1981), ya que disminuyen el tiempo de uso de las praderas, causando pérdidas en el peso de los animales y en la producción de leche (Ramos, 1977). Para 1983, las pérdidas debidas a la plaga se estimaron en 450 millones de pesos en la zona de Villavicencio - Meta¹.

Las prácticas de manejo de las "salivitas" o "miones", empleadas hasta el momento, no han sido completamente eficientes, por lo cual es conveniente buscar otras alternativas de control. Entre ellas está el control mediante el uso de enemigos naturales, entre los cuales la especie *Salpingogaster nigra* Schiner (Diptera: Syrphidae) ofrece buenas posibilidades si se considera que en Brasil (Guagliumi, 1970), Colombia (Jiménez, 1978) y Trinidad (Guppy, 1913) este predator ha sido reportado como eficiente enemigo natural de Cercópidos, su cría masiva y liberación podría hacer una práctica efectiva para controlar esta plaga.

Como en Colombia no se ha efectuado un estudio biológico de esta especie benéfica, se realizó el presente trabajo pretendiendo con ello aportar un elemento más a la estructuración de un programa de manejo integrado de los "miones" o "salivita". Los objetivos del estudio fueron: realizar observaciones sobre los hábitos, comportamiento y posibles enemigos naturales del predator *Salpingogaster nigra*, y determinar el ciclo de vida y evaluar a nivel de laboratorio su capacidad como predator de ninfas del "mion" de los pastos.

MATERIALES Y METODOS

Las observaciones se realizaron en fincas de Brachiaria de la finca "San José" en Medina (Cund.) (T = 27°C, H.R. = 85%) y del Centro Regional de Investigaciones "La Libertad" del ICA en Villavicencio (Meta) (T = 25°C y H.R. = 85%), ubicados entre los 400 - 500 m.s.n.m. Se confirmó la especie del Díptero por comparación con especímenes de la Colección del Programa de Entomología del CRI "La Libertad", muestra número 563. Para obtener información sobre biología, hábitos y comportamiento del *S. nigra*, cada uno de los estados fue observado en condiciones naturales; al mismo tiempo se colectó material para estudiarlo en laboratorio y establecer la duración de cada estado.

* Estudiante Facultad de Agronomía, Univ. Nacional, Bogotá.
** Ingeniero Agrónomo, M. Sc., Sanidad Vegetal, ICA, Bogotá.
*** Biólogo, Facultad de Agronomía, Univ. Nacional, Bogotá.

¹ Mendoza, P. Comunicación personal. ICA, Programa de Pastos y Forrajes, Bogotá, 1983.

La determinación del número de instares de la fase larval se hizo estadísticamente por morfometría del esqueleto cefalofaríngeal (Lawrence, 1979), tomando como dimensiones básicas la longitud y ancho de los ganchos bucales; adicionalmente se midió la longitud y ancho de los espiráculos caudales, y la longitud y ancho de las larvas. Se disectaron y midieron 230 larvas de diferentes tamaños y con la información obtenida se elaboraron las distribuciones de frecuencia que fueron graficadas y analizadas para determinar el número de instares larvales. Se calculó una función de regresión lineal múltiple para correlacionar longitud, ancho y edad de las larvas, y por medio de ella se estimó la edad y duración del estado larval.

Para determinar la capacidad de predación del díptero sobre ninfas del "mión", se colocó una larva por vaso plástico, y se le suministró diariamente ninfas de diferentes tamaños. Al mismo tiempo se retiraban las ninfas que habían muerto, para observarlas al estereoscopio y verificar si habían sido atacadas por las larvas. El cálculo de la capacidad de predación de las larvas se hizo utilizando como estimador, el promedio de ninfas consumidas por larva por día.

En el campo se efectuaron muestreos de las poblaciones, tanto del "mión" como del predador *S. nigra*. Para los estados inmaduros se hicieron 3 muestreos diarios con un marco de madera de 1 m², y para los adultos 10 pases dobles de jama en 3 sitios diferentes, para luego buscar una relación con respecto a los factores climáticos: temperatura, humedad relativa y precipitación, que se tomaron a las 7 am, 12 y 4 pm.

RESULTADOS Y DISCUSION

CICLO DE VIDA

HUEVO

Los huevos se encuentran entre la espuma secretada por las ninfas del "mión", principalmente en la localizada sobre las raicillas. Son de aspecto lechoso, ovalados, con algunas estrías superficiales y achatados en los extremos. Miden en promedio 0,85 mm de largo x 0,35 mm de ancho en la parte más abultada; tienen una duración promedio de 2,7 días con una variación de dos a cuatro días. Se obtuvo un porcentaje de eclosión del 58,4%. Al acercarse la eclosión se diferencian sobre la superficie zonas translúcidas y lechosas.

LARVA

La larva es recta, delgada, áпода, achatada en el extremo posterior, tipo brachíptera, sin una diferenciación del cefalotórax del resto del cuerpo. Recién nacida mide cerca de 1 mm de largo x 0,4 mm de ancho; es translúcida, con ganchos bucales negros, bien diferenciados y esclerotizados que se desplazan en un plano horizontal. A medida que se desarrolla se torna de color crema o marfil y está recubierta de una sustancia mucosa. El aparato digestivo es de color anaranjado o rojo. Al acercarse en empupamiento, en el aspecto dorsal aparecen unas manchas parecidas a gránulos blancos que corresponden al cuerpo graso. También son visibles



FIGURA 1. Larvas de *Salpingogaster nigra* en diferentes estados de desarrollo; del primer al tercer instar. (Foto: A. Acosta).

los espiráculos caudales que en larvas pequeñas tienen forma de bastón y están bien separados, mientras que en las bien desarrolladas aparecen soldados y en forma de frijol (Fig 3). En la Figura 1 se aprecian algunas larvas en diferentes estados de desarrollo. En el campo las larvas se encuentran entre la espuma producida por el "mión", principalmente en aquella ubicada cerca de las raíces y se alimentan de ella o de las ninfas. Las larvas se desplazan con igual facilidad sobre superficies lisas o rugosas.

Aunque sólo fue posible hacer el seguimiento hasta pupa a 4 larvas, con base en las 72 medidas del ancho y largo de ellas se calculó y generalizó una función de regresión lineal múltiple para llegar a la siguiente ecuación: $E = 0,68 + 1,4685 (AL) + 0,2427 (LT)$, con un $r^2 = 0,977$; donde AL = ancho de la larva, LT = largo total de la larva. El alto valor de r^2 indica un buen ajuste de la ecuación de regresión propuesta. Con esta ecuación se estimó la edad de 230 larvas disectadas, y se logró establecer que el período larval tiene una duración total de 9,7 días. En promedio, las larvas de tercer instar miden 12,9 mm de largo por 3,42 mm de ancho.

Las distribuciones de frecuencia con las diferentes variables muestran tres picos correspondientes a los tres instares por los que pasa el estado larval. En la Figura 2 aparece el polígono de frecuencias correspondiente al ancho de los ganchos bucales de 230 larvas y en la Figura 3 se presentan las dimensiones promedio y forma de los ganchos bucales y espiráculos de cada instar, y la variación de las dimensiones se resume en la Tabla 1.

Una vez que la larva está lista para empupar, reduce notablemente su movilidad, y elimina el contenido del tracto

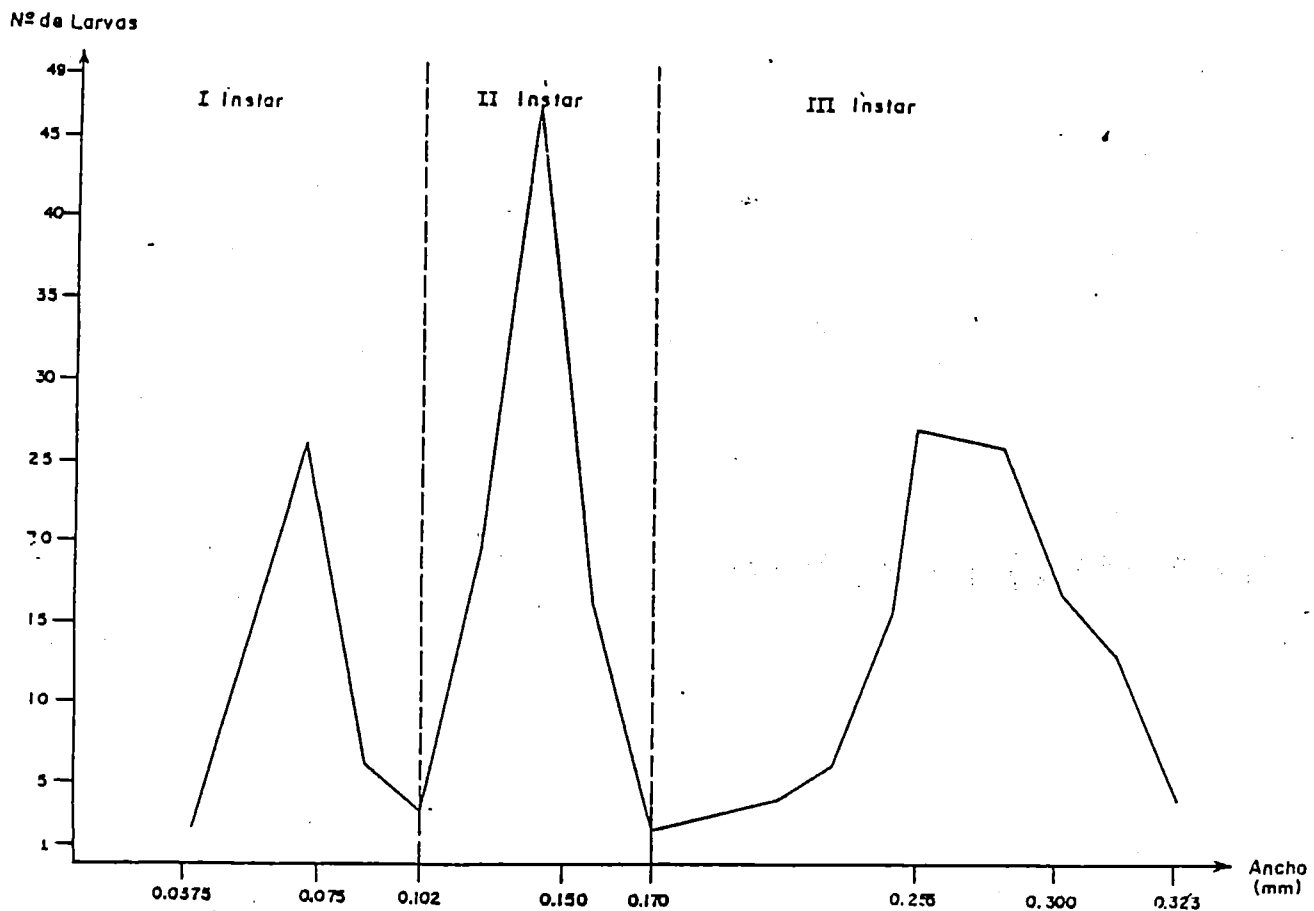


FIGURA 2. Polígono de Frecuencias del ancho de los ganchos bucales de 230 larvas de *Salpingogaster nigra*.

digestivo. La larva se fija a la superficie de empupamiento que generalmente es un tallo u hoja del pasto en descomposición y comienza a recogerse hasta adquirir la forma de pupa, la cual inicialmente es de color marfil. Este proceso tuvo una duración entre 2 y 6 horas.

TABLA 1. INSTARES LARVALES DE *Salpingogaster nigra* DETERMINADAS CON BASE EN LAS DIMENSIONES DE LOS GANCHOS BUCALES Y LOS ESPIRÁCULOS DE 230 LARVAS.

	I Instar		II Instar		III Instar	
	min.	max.	min.	max.	min.	max.
Ganchos bucales						
Ancho mm	0,034	0,085	0,119	0,170	0,204	0,323
Largo mm	0,140	0,250	0,360	0,580	0,650	0,880
Espiráculos						
Ancho mm	0,010	0,050	0,070	0,140	0,170	0,340
Largo mm	0,030	0,130	0,140	0,350	0,360	0,660

PUPA

La pupa bien formada se va quitinizando y va tomando una tonalidad parda cada vez más oscura. Dorsalmente aparecen 4 puntos negros y lateralmente resaltan dos arcos de color café claro. La pupa es gutiforme con aspecto de mazo (Fig. 4); mide en promedio 9,01 mm de longitud por 3,4 mm de ancho en la parte más abultada y bajo condiciones de laboratorio tienen una duración promedio de 9,67 días. En el campo comúnmente se le encuentra adherida a trozos de material vegetal en descomposición sobre el suelo. Al acercarse la emergencia, la cual se efectúa entre las 7 - 9 am, se observan los ojos del adulto en la parte más abultada. Bajo condiciones de laboratorio se obtuvo un porcentaje de emergencia del 39,47%.

ADULTO

Los adultos son de color negro con aspecto de avispa; cuerpo alargado; aparato bucal chupador; tienen dos bandas amarillas en la cabeza, dos en los costados del tórax y uno en el tercer segmento tarsal de todas las patas (Fig. 5). Miden de largo 1,5 cm. La especie presenta dimorfismo sexual,

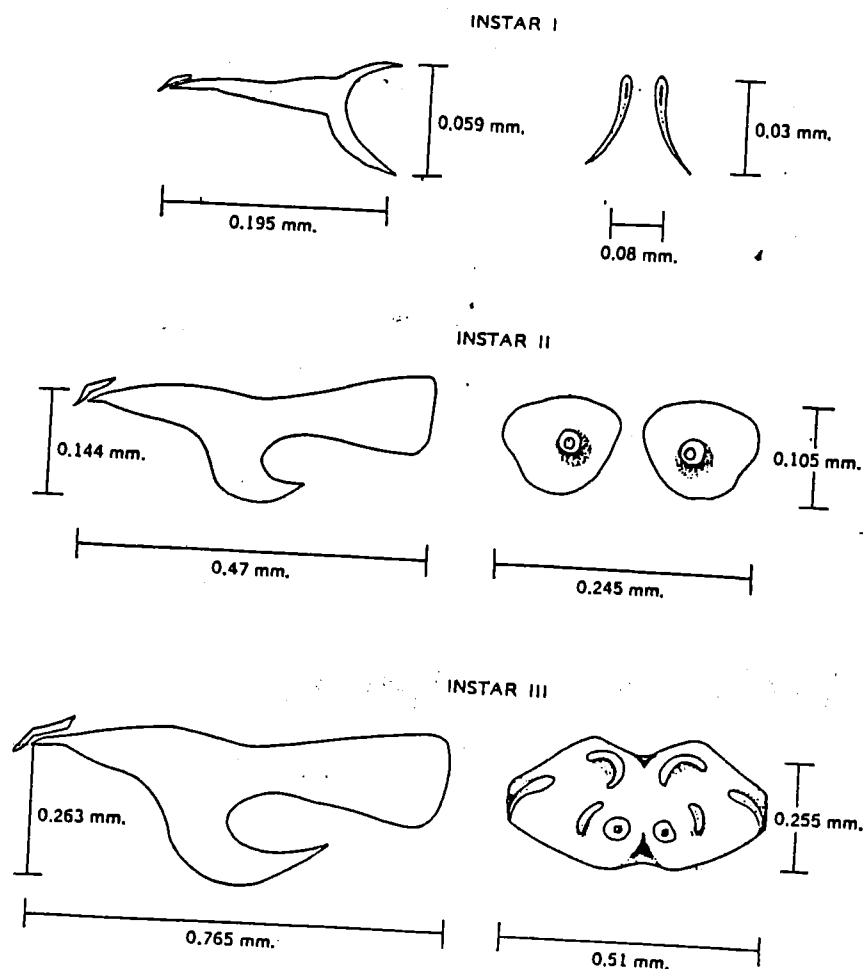


FIGURA 3. Forma y dimensiones $\bar{x}$, de los ganchos bucales y los espiráculos de cada instar.

siendo la terminación del abdomen más aguda en la hembra, y los ojos son más prominentes también en las hembras (Figura 6).

Aunque la duración real del adulto no pudo ser determinada en laboratorio, se encontró una mayor longevidad en la hembra (5,2 días) que en el macho (4,9 días). Durante el día frecuentan flores de vegetación herbácea y arbustiva en sitios húmedos, frescos y sombreados en busca de alimento y protección; también se les observa en las praderas cuando el ambiente es fresco.

El apareamiento se efectúa entre las 10 am y las 3 pm, en zonas sombreadas cercanas a la pradera o dentro de ésta. Antes del apareamiento los machos se tornan inquietos y dominan un territorio, el cual defienden, esperando que llegue una hembra para copular.

Para la oviposición, la hembra busca espumas del "mión", las examina y luego introduce su abdomen dejando entre 1 y 14 huevos por espuma, colocados individualmente. Una hembra en observación durante el período de oviposición, ovipositó en cinco ocasiones en un lapso de 30 minutos.

En resumen el ciclo de vida del predador *S. nigra* tiene una duración promedio de 27,39 días.

EVALUACION DE LA CAPACIDAD DE PREDACION

Después de hacer el seguimiento de 24 larvas y el consumo de ninfas durante el período larval se encontró que el pro-

medio de ninfas consumidas por una larva fue de 17,20. El intervalo de confianza para la media del consumo de ninfas durante el estado larval, con una confiabilidad del 90% fue (14,4592; 19,9574).

Esta información difiere de lo encontrado por Guppy (1913) quien reporta un consumo de 30 a 40 ninfas por larva durante 9 a 19 días que dura la fase larval.

Durante la realización del trabajo bajo las condiciones del laboratorio se presentaron problemas de contaminación del material vivo. Lo más frecuente fue la presencia de un nemátodo que atacó huevos, larvas y pupas de *S. nigra*, el cual posiblemente era transportado al laboratorio entre las espumas colectadas en el campo y que se utilizaron para mantener las larvas en cautiverio. También se presentó una mosquita de la familia Phoridae que ataca las pupas. Otro agente contaminante de pupas colectadas en campo fue el hongo entomopatógeno *Metarhizium* sp. Por otro lado, el desconocimiento de los factores abióticos óptimos para mantener el material vivo en cautiverio ocasionó la pérdida de buena cantidad de él. Las larvas con baja humedad y alta temperatura se deshidratan rápidamente, mientras que el exceso de humedad ocasiona malos olores que atraen agentes contaminantes.

En el campo se observaron dos enemigos naturales de los adultos de *S. nigra*, pero no se logró su identificación. Se trata de una hormiga de color negro, de aproximadamente



FIGURA 4. Pupas de *Salpingogaster nigra*. (Foto: Autores).

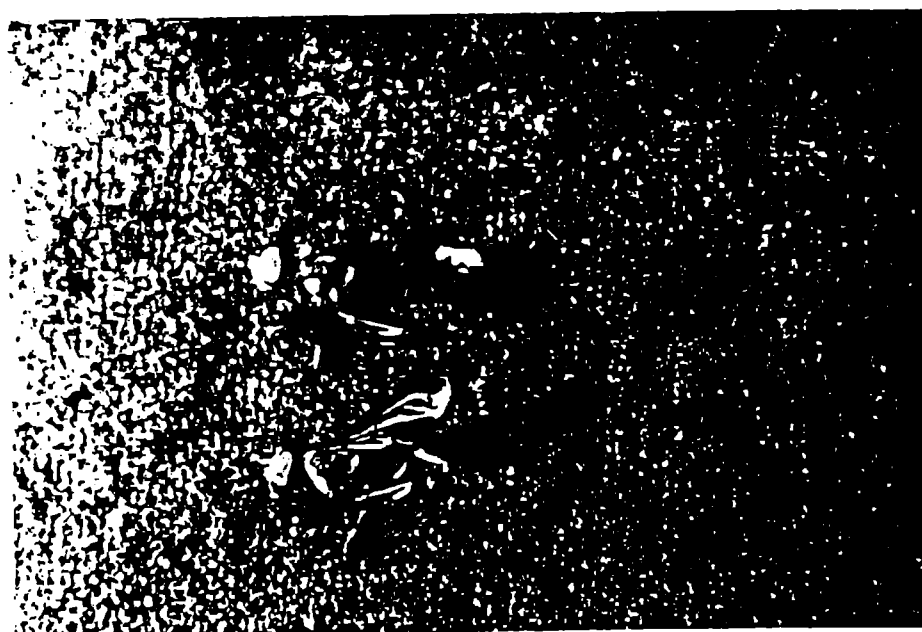


FIGURA 5. Adultos de *Salpingogaster nigra*. En la parte superior el macho y abajo la hembra. (Foto: Autores).

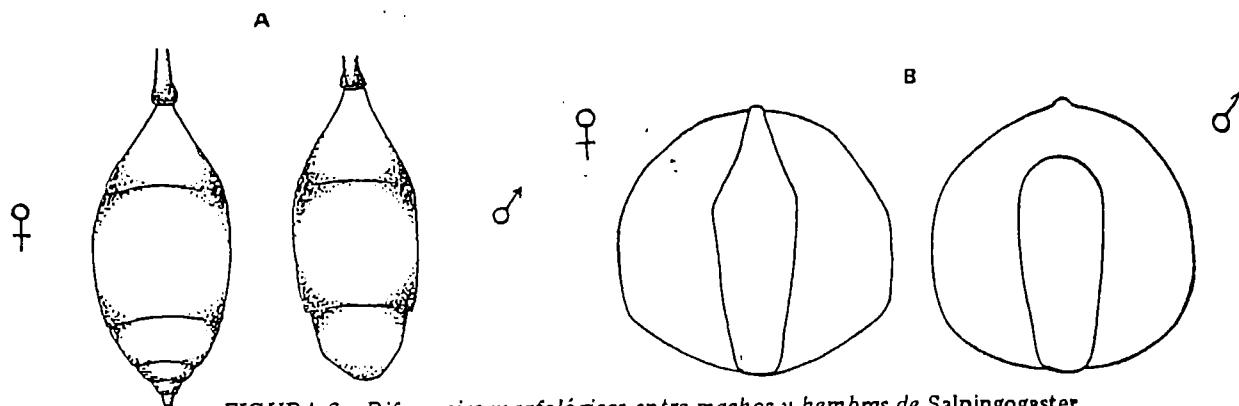


FIGURA 6. Diferencias morfológicas entre machos y hembras de *Salpingogaster nigra*. A. Vista dorsal del abdomen. B. Vista frontal de los ojos.

1,5 cm de longitud, que los agricultores denominan "hormiga zorra", la cual ataca adultos recién emergidos del pupario; también se observaron algunas arañas habitantes de la pradera que atrapan los adultos en sus redes. Por otro lado se encontró un díptero negro y pequeño que emergió de pupas colectadas en el campo.

CONCLUSIONES Y RECOMENDACIONES

La especie *Salpingogaster nigra* Schiner (Diptera: Syrphidae), de acuerdo con el análisis morfométrico del aparato cefalofaríngeal, presenta tres instares durante la fase larval. Además, el instar en que se encuentra una larva puede determinarse fácilmente por la forma de los espiráculos, ya que estos son diferentes en los tres instares.

La sobrevivencia del *S. nigra*, depende casi totalmente del "mión" de los pastos ya que el estado de huevo se localiza en las espumas, y las larvas se alimentan de ninfas de la plaga. Durante la fase larval, un individuo de *S. nigra* puede llegar a consumir en promedio 17,04 ninfas.

Se reconocieron como enemigos naturales del estado adulto de *S. nigra* una hormiga y arañas que habitan en la pradera. También se encontró un díptero como parásito de pupas.

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Natural History of the Spittlebug *Prosapia* nr. *bicincta* (Homoptera: Cercopidae) in Association with Dairy Pastures of Costa Rica

DANIEL C. PECK

Department of Entomology, Cornell University, Ithaca, NY 14853

Ann. Entomol. Soc. Am. 91(4): 435-444 (1998)

ABSTRACT The natural history of *Prosapia* nr. *bicincta* was examined in upland dairy pastures of Costa Rica where it feeds on *Cynodon nlemfuensis* Vanderyst (East African star grass) and *Pennisetum clandestinum* Hochst. (kikuyu grass). Aspects of the biology and behavior are described, including identification and characterization of instars, feeding habits, and reproductive biology. In this habitat, *P. nr. bicincta* demonstrated an extended nymphal stage and preoviposition period compared with other *Prosapia* and grassland cercopids. Nymphs required 34-98 d (mean 62.7) to complete 5 instars under greenhouse conditions. The 1st instars specialized on surface roots whereas older instars expanded their range of feeding sites to include mature stems. In the greenhouse, adults lived up to 7 wk, initiated mating as soon as 18 h after emergence, had a 15-22-d preoviposition period, and were capable of producing up to 16 eggs in 1 day. Oviposition sites were almost exclusively in the soil. In a preference experiment females laid more eggs in bare versus litter-covered soil, but in a no-choice experiment presence of litter enhanced oviposition. Life stage-specific data on *P. nr. bicincta* will guide improvements in pest management. New information from this species also expands our understanding of variation in cercopid natural history and highlights the need to delineate differences, in addition to commonalities, among the species in this pest complex.

KEY WORDS *Cynodon nlemfuensis*, *Pennisetum clandestinum*, Costa Rica, forage grass, frog hopper, spittle mass

ACCOUNTS OF HOMOPTERAN pests inadequately consider the horticultural, biological, and economic impact of spittlebugs and frog hoppers from the family Cercopidae (sensu Metcalf 1961). In the New World tropics, grassland cercopids attack some of the most widely sown grasses of improved pastures, including *Brachiaria* (Ferrufino and Lapointe 1989), kikuyu (*Pennisetum clandestinum* Hochst.) (Fagan and Picado 1971), and coastal Bermuda grass, *Cynodon dactylon* (L.) (Byers 1965, Fagan and Kuitert 1969); as well as other graminaceous crops such as sugarcane, *Saccharum officinarum* (L.) (Williams 1921, Guagliumi 1973); rice, *Oriza sativa* (L.) (Souza and Nilakhe 1985); and turfgrass (Poaceae spp.) (Tashiro 1987). Throughout their range, these native insects are regarded as the most destructive pests in pastures and the 2nd most destructive pests in sugarcane plantations.

In rangelands, grassland cercopids compete with grazing animals by reducing forage availability and quality (Valério and Nakano 1988). Outbreaks of these insects prevent the establishment and lower the persistence of improved forages (Taliaferro et al. 1967, Valério and Nakano 1987). Adult feeding induces a destructive phytotoxemia called frog hopper burn (blight) in susceptible plants of pastures and cane fields (Fewkes 1963, Byers and Wells 1966, Valério et al. 1988). Cercopids of the expansive rangelands of the Colombian Llanos, for instance, limit the establishment of *Brachiaria* grasses, which are well adapted to

the poor soils and climate of the region (Lapointe et al. 1992). Grassland cercopids thereby reduce the efficiency of land use for dairy and beef cattle production.

Cercopids are long-lived, xylem-feeding insects that make a heavy biological investment in self-defense. Nymphs (spittlebugs) live in spittle masses as protection from adverse microclimate and enemies (Whitaker 1970). These shelters are constructed by adding hundreds of bubbles to feeding wastes that are stabilized by the presence of mucopolysaccharides and polypeptides (Marshall 1966, Mello et al. 1987). Although no longer capable of producing spittle, most adults (frog hoppers) display warning colors and have the ability to bleed reflexively (Peck 1996) and jump to evade enemies.

Most individual tactics to control grassland cercopids have been short-lived or ineffective. Host plant resistance is 1 tactic that may remediate spittlebug problems in many regions (Ferrufino and Lapointe 1989, Lapointe et al. 1992, Miles et al. 1995), but there will be a continued need to manage susceptible varieties of forage grasses. Integrated pest management strategies (Valério and Koller 1993) have met with little success. The underlying failing may be the tendency to regard grassland cercopids as a homogeneous pest complex. Rather than focus on similarities, the differences among species should be elucidated through examinations of cercopid life styles under local conditions. When the taxonomic diversity of the

group is superimposed on the range of ecological zones in which they occur, it becomes clear that cercopids engage in widely varying associations with their particular habitats. Therefore, despite the commonalities of the grassland habitat, the nature of the pest's impact varies among regions. In consequence, the outcome of management tactics, such as host plant resistance, also varies regionally.

The genus *Prosapia* ranges from southern Ontario to Panama (Hamilton 1977, 1982). It is the northernmost taxon of the economically important New World Cercopidae that includes *Aeneolamia*, *Deois*, *Mahanarva*, *Notozulia*, *Sphenorhina*, *Tomaspsis*, and *Zulia*. Hamilton (1977) describes 14 species of *Prosapia*, 3 of which have received considerable attention for their status as forage pests: *P. bicincta* (Say) across the southeastern United States, *P. simulans* (Walker) from Mexico to Costa Rica, and *P. plagiata* (Distant) (= *P. distantii*) in Costa Rica.

Cercopids were 1st reported as pests in Costa Rica in the late 1940s (Picado 1970, Fagan and Picado 1971). One species of *Zulia*, 4 *Aeneolamia* and 4 *Prosapia* currently damage pastures and sugarcane fields (Thompson 1996). In the Monteverde region of Costa Rica, the predominant pest of forage grasses is a currently undetermined species of *Prosapia* related to *P. bicincta* but distinct from this species and other Costa Rican congeners (hereafter called *P. nr. bicincta*). Current taxonomic studies suggest it is undescribed (V. Thompson, personal communication). In the early 1960s, outbreaks of this species forced a conversion from the susceptible forage, kikuyu grass, to a more tolerant forage, East African star grass (*Cynodon nlemfuensis* Vanderyst). *P. nr. bicincta* has resurged to pest status over the last decade because control tactics have largely failed to reduce populations below economic injury levels. Despite this, *P. nr. bicincta* has not been the focus of any published study.

These investigations aimed to describe the natural history of *P. nr. bicincta* in intensively grazed upland dairy pastures. I sought to elucidate aspects of the biology and behavior relevant to its pest status, including description of instars, feeding habits, and reproductive biology. In particular, this study examined the habits, requirements, and preferences of the life stages. The results further our understanding of the variation in the biology and behavior of this group and will guide improvements in spittlebug management based on species and life-stage-specific understanding.

Materials and Methods

Habitat and Site Descriptions. These investigations focused on populations of *P. nr. bicincta* located in the Tilarán Mountains of north central Costa Rica. Monteverde is a seasonally wet region between 1,300 and 1,600 m above sea level within the tropical premontane and lower montane cloud forest life zones. The landscape is a mix of forest, coffee and banana patches, and dairy pastures dominated by East African star grass, kikuyu grass and pitilla (*Sporobolus* spp.). Field

observations were carried out during the wet seasons of 1991–1994 (May–September) in star grass pastures managed with intensive rotational grazing. One paddock, C2, was the site of many of the following field studies and was representative of the habitat in which *P. nr. bicincta* occurs as a pest. C2 was 0.21 ha, centrally situated among 19 predominantly star grass paddocks; 1,355–1,385 m in elevation; and surrounded by forest. Star grass in C2 was interspersed with the clump grass pitilla (~5% surface area) and other weedy herbaceous species (~5%). Every 2–3 wk during the wet season, C2 was grazed by ~40 cows for 4 h.

Three other grassland cercopids co-occur with *P. nr. bicincta* in the pastures of Monteverde. *P. plagiata* appears to prefer forest edges and higher elevations; throughout Costa Rica this species is most abundant at 1,450–2,000 m in elevation (Washbon 1968). *P. simulans* does not complete its life cycle in the zone but occurs as male immigrants that arrive from lower-elevation breeding grounds (Peck 1996). This species occurs throughout Costa Rica at coastal and low-elevation sites (Thompson 1996). *Aeneolamia postica* (Walker) also occurs in the zone but is uncommon.

Morphological Measurements. To facilitate initial discrimination among instars, I used an ocular micrometer to measure the width of the head capsule where it intersected the hind margin of the eyes. Head capsule width is diagnostic of instar for other spittlebug taxa (Byers 1965). In 1991, 295 nymphs were arbitrarily chosen for measurement from field-collected individuals that had been killed and stored in 70% EtOH.

Once it was possible to determine instar with head capsule measurements, I made further morphological measurements of field-collected nymphs and adults in 1994 to characterize the differences among the life stages. Head capsule width was the widest distance across the compound eyes (equally as wide as across the hind margin of the eye, but easier to measure); body length, the maximum distance from the tip of the head to the end of the abdomen (nymphs), wing (adult males), or ovipositor (some adult females); body width, the maximum width across the body (usually just posterior to the posterior wing stripe) with wings at natural repose (adults only); stylet length, the distance from the distal end of the labrum to tip of the styli; and wing pad length, the maximum length of the developing wings (3rd through 5th instars only). Nymphs were killed by and stored in 70% EtOH; some adults were frozen before storage in alcohol.

Spittle Mass Site and Size. I investigated the availability of feeding sites for each instar by surveying spittle masses in areas dominated by star grass but interspersed with nonforage species within the foraging ambit of nymphs (1992–1993). The census did not include spittle masses on kikuyu or pitilla or those with multiple occupants. For each spittle mass, the instar of the occupant and 1 of the following sites on star grass was recorded: mature stem (>22 cm long), young stem (<22 cm long), stolon (connection between 2 rooted runners or stems), surface secondary root (of stem or runner), and aerial (not touching the soil or

litter layer). Aside from length, young and mature stems largely differed in toughness, not diameter, because old stems also could be slender. The occurrence of nymphs on nonforage species also was recorded.

Spittle mass sizes were calculated by measuring the average diameter of masses housing individual spittlebugs at sites in the field and in laboratory pots. No attempt was made to control for environmental conditions that could have influenced spittle mass size.

Stadia Determination. The time required to pass through instars was determined by following individuals isolated on potted star grass under ambient temperatures. Every 1–2 d, I used forceps to gently remove the nymphs part way from their spittle masses, visually determined their instar, and replaced them. This assessment only temporarily disturbed the nymphs and did not force them to reconstruct spittle masses. Because of their more restrictive feeding and microclimate requirements, the stadia of 1st instars was determined under special conditions. Recently hatched nymphs were housed in large petri dishes lined with a double layer of filter paper kept very moist. Star grass cuttings with attached secondary roots were added to provide adequate sites for construction of spittle masses. Nymphs were transferred to pots after molting to the 2nd instar.

Reproductive Biology. Chambers and sleeve cages were used to observe adults under ambient conditions of light, temperature, and humidity. Chambers were constructed from plastic ice cream tubs (0.9–3.8-liter volume) by replacing the lid and the bottom with fine netting. Three to 6 holes in the wall were made so that water piks fit snugly at the horizontal with their opening just within the cage and the tubes protruding to the outside. Each pik held water and 1–3 cut sprigs of star grass that were available to the caged adults. Froghoppers survived as long as 15 d with replacement of cuttings every 2–3 d. Females readily oviposited in cotton that was wrapped around the stems to support the bouquet in test tubes substituting for the piks. The cotton remained moist through its contact with the water in the tubes, and eggs were separated from the material with the aid of a dissecting scope. Populations of froghoppers also were maintained successfully in the greenhouse on potted star grass enclosed in sleeve cages sewn from insect netting.

Estimates of premating period, time in copula, and number of copulations were made by observing newly emerged teneral females every 1–3 h while held in chambers with males. Preoviposition period was estimated from small groups of newly emerged teneral females (3–5) held in chambers or sleeve cages with males (4–5). Adults from sleeve cages were placed periodically in oviposition chambers to determine the time of 1st oviposition. Estimates of adult life span were made by following the survival of newly emerged tenerals housed in groups of 1–10 in sleeve cages.

To determine oviposition sites, field-collected females were held in sleeve cages over large pots (plastic, 16 cm diameter) of star grass with a bare soil or litter-covered surface. Of 2 litter free pots (1992), 1 contained 16 star grass stems with 40–50 adults of

mixed sex for ≈ 4 d whereas the other contained 21 stems with ≈ 180 females for 1–2 d. Three litter-covered pots (1993) contained 15, 21, and 16 stems and housed groups of 15, 16, and 17 females for 48 h. A 1-cm-thick layer of litter (dry star grass cut into 1-cm lengths) was added to the top of a 2.5-cm-thick layer of soil that had been passed through a wire mesh with holes 1 by 1 mm. Both layers were moistened with tap water.

After the females were removed, eggs on the plant stem and under leaf sheaths were located directly by using a dissecting microscope. Eggs were separated from the soil by flotation in saturated salt solution and from the litter by washing in water, drawing off the bottom of a separatory funnel and floating in salt solution.

Oviposition Experiments. Because *P. nr. bicincta* control measures in Monteverde feature controlled grazing and fertilization, the effect of soil cover and fertilizer levels on female oviposition behavior was tested in 1 preference and 1 no-choice experiment.

In the 1st experiment, oviposition preferences were tested by enclosing groups of females in greenhouse cages for 72 h where they were offered a choice of 4 star grass pots (peat, 8 cm diameter). The experimental design was a 2×2 factorial where soil cover treatments of soil or litter were combined with fertilizer treatments of fertilized or not fertilized. Soil and litter pots were prepared as above, except that soil was passed through a screen with mesh size 1.5 by 2 mm and packed to 1 cm deep, whereas litter was added to the top of an unprepared soil surface. Fertilizer treatments were prepared 5 d before the start of the experiment with 0.264 g of 10–10–10 granular fertilizer dissolved in water, ≈ 4 times the concentration typically added to pastures after grazing bouts (≈ 130 kg/ha) to increase the opportunity of a plant response. Unfertilized pots were watered.

One pot of each of the 4 treatment combinations was placed in a shallow plastic tub and covered with a wire screen cage (35 cm tall, 22 cm diameter). The treatments were positioned so that all the pots were touching but the plants were not. The fertilizer treatments were randomly assigned after pots with soil surface were placed opposite one another. Female *P. nr. bicincta* were collected from the field the day before the start of the experiment and maintained in sleeve cages overnight. Twenty females were added to each of the 10 replicate cages and 4 times every day (≈ 0600 , 1100, 1500, and 1900 hours) their position on the pots was noted by counting those individuals on the plants and those touching the soil or litter substrate. Plants were watered after 36 h; all froghoppers were removed after 72 h. Eggs were extracted from the plant, litter and soil as in the previous section. Plant height and dry mass were measured.

In the no-choice experiment, the effect on oviposition rate was tested by enclosing groups of females in sleeve cages placed over individual pots of star grass (plastic, 12.5 cm diameter) (1992). Six treatment combinations were evaluated based on 2 surface treatments (soil and litter prepared as above) and 3 fer-

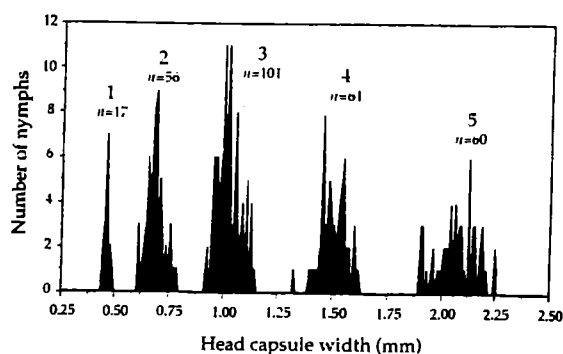


Fig. 1. Frequency distribution of nymphal head capsule widths of *P. nr. bicincta*.

tilizer levels (applied as above): a control with no fertilizer, low level with 0.161 g of fertilizer approximating concentrations applied to fields, and high level with 0.644 g approximating 4 times field levels. Ten field-collected females were added to sleeve cages placed over 30 pots assigned to 5 replicates of all 6 treatment combinations. After 72 h females were removed and eggs extracted from the plant, 1 cm prepared soil, litter, and a 1-cm-layer of unprepared soil under litter. Plant height and dry mass were measured.

Both experiments were carried out under ambient conditions of light, temperature, and humidity. Analysis of variance (ANOVA) was used to test for the effect of soil cover and fertilizer level on plant (feeding) and substrate (oviposition) activity (preference experiment), and the number of eggs laid per female (no-choice experiment, square-root transformed). The full factorial model was reduced through analysis of sequential (Type I) sums of squares; plant dry mass was retained as a covariate. In the preference experiment, the effect of each treatment factor on the number of eggs laid per female was tested independently with the Wilcoxon rank-sum nonparametric test because data could not be normalized through any standard transformation. In calculations of oviposition rate all females that disappeared or died during the oviposition period were counted as only half a female. In litter treatments of the no-choice experiment, ANOVA was used to test for the effect of fertilizer

level on the proportion of eggs laid in the litter and soil layers.

Results

Nymphal Morphology. *P. nr. bicincta* had 5 instars that could be reliably distinguished in the field without magnification. The nonoverlapping frequency distribution of head capsule widths indicated 5 size classes (Fig. 1). Several morphological measures varied from 1 instar to the next. From 1st to 5th instar, head capsule width, body length, stylet length, and wing pad length all increased (Table 1). Late 5th instars (5b, within 3 d of molt to the adult) were significantly longer than early 5th instars (5a) and were easily differentiated by adult pigmentation on the thorax and wing pads.

Nymphal Biology. Nymphs surrounded themselves with masses of spittle at their feeding sites low in the pasture sward. Spittlebugs clung to the stem with all 6 legs, using the tarsal claws and distal tarsal spines, while the telescoping abdomen reached as far as the metacoxa to place individual bubbles. The normal head down position encouraged the spread of feeding wastes and spittle bubbles from the tip of the abdomen over their bodies and feeding sites. When two 5th instars were forced to remake spittle masses, they were capable of 16 and 27 bubbles per minute, completing coating themselves with spittle in 15 min. Bubble size appeared to increase with instar. The overall volume of the spittle mass also increased with instar. Mean diameter ($\pm$ SE) for instars 1–5 were 2.44 ± 0.14 , 3.90 ± 0.23 , 5.50 ± 0.21 , 10.68 ± 0.74 , and 14.84 ± 0.48 mm, respectively (Fig. 2). Both served as additional characters that assisted in field determinations of instar. Of 2,933 spittle masses examined in population surveys (Peck 1996), 7.67% had multiple (2–5) occupants. These combined masses grew very large: 1 spittle mass housing four 5th instars had a mean diameter of 3.5 cm.

The 5 instars also varied in their selection of feeding sites. These sites on star grass shifted with increasing instar from secondary roots to young stems, to stolons and mature stems (Fig. 3). Early instars, in particular, regularly made spittle masses on the basal stem and secondary roots of nonforage species that substituted

Table 1. Size of nymphal and adult life stages of *P. nr. bicincta*.

Life stage	n	Head width, mm	Body length, mm	Body width, mm	Style length, mm	Wing pad length, mm
Instar 1	30	$0.47 \pm 0.006a$	$1.76 \pm 0.038a$		$0.38 \pm 0.005a$	
Instar 2	28	$0.71 \pm 0.006b$	$2.72 \pm 0.050b$		$0.52 \pm 0.008b$	
Instar 3	30	$1.04 \pm 0.008c$	$4.23 \pm 0.079c$		$0.78 \pm 0.011c$	
Instar 4	30	$1.53 \pm 0.013d$	$6.27 \pm 0.127d$		$1.13 \pm 0.013d$	$0.40 \pm 0.006a$
Instar 5a	30	$2.12 \pm 0.012e$	$9.08 \pm 0.145e$		$1.60 \pm 0.013f$	$1.01 \pm 0.013b$
Instar 5b	30	$2.10 \pm 0.013e$	$10.23 \pm 0.105fg$		$1.64 \pm 0.020f$	$2.72 \pm 0.031e$
Adult male	45 (30 stylet)	$2.28 \pm 0.012f$	$10.69 \pm 0.075g$	$4.80 \pm 0.036a$	$1.20 \pm 0.015e$	$2.83 \pm 0.042c$
Adult female	33 (32 stylet)	$2.48 \pm 0.014g$	$9.48 \pm 0.084f$	$5.06 \pm 0.061b$	$1.24 \pm 0.013e$	

Instar 5 is separated into early (5a) and late (5b) stages. Within a column, means ($\pm$ SE) followed by different letters are significantly different at $P < 0.05$. Differences in body width were determined by Wilcoxon rank-sum nonparametric test; all others determined with Tukey-Kramer HSD test for multiple comparisons (square-root transformed).

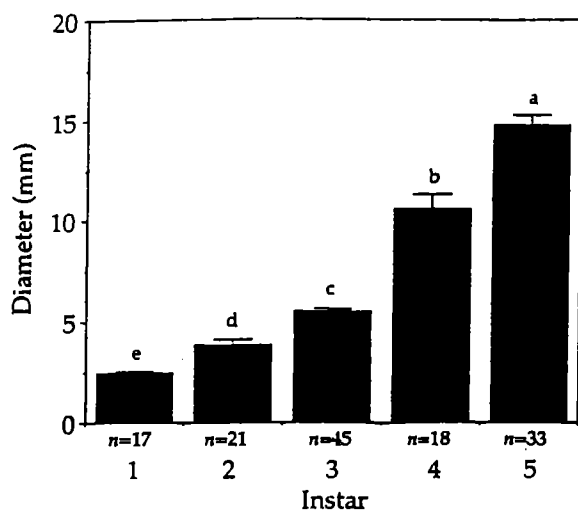


Fig. 2. Diameter of spittle masses produced by 5 instars of *P. nr. bicincta*. Bars are standard errors and different letters represent means significantly different at $P < 0.05$ (Tukey-Kramer HSD test for multiple comparisons).

for star grass secondary roots as adequate sites for spittle mass establishment.

Teneral adults were almost always found inside the spittle mass of the 5th instar. New tenerals were soft and pale white. In many instances it was clear a special spittle mass had been constructed de novo for this final molt. This spittle had a hollow shape and was frequently found at aerial sites on grass blades where other spittle masses rarely occurred. Other instars molted within the spittle mass without an air pocket. Nymphs either remained in the same spittle mass, to which the old exoskeleton clung, or moved to new

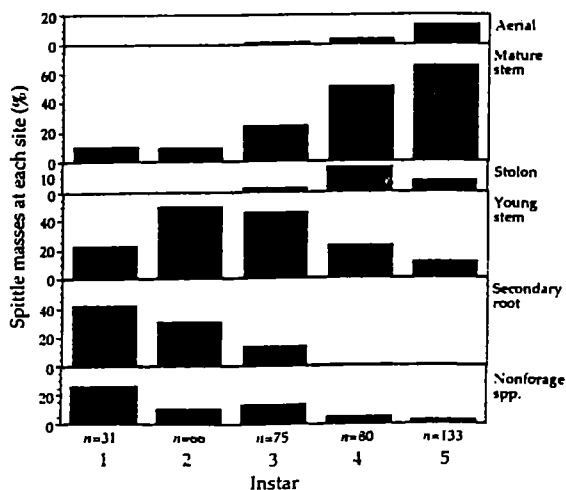


Fig. 3. Distribution of spittle masses of *P. nr. bicincta* on host plants. Only sites on East African star grass and nonforage hosts were recorded. Nonforage species included *Kyllinga* spp. (Cyperaceae), *P. conjugatum* (Poaceae), and *D. abyssinica* (Poaceae).

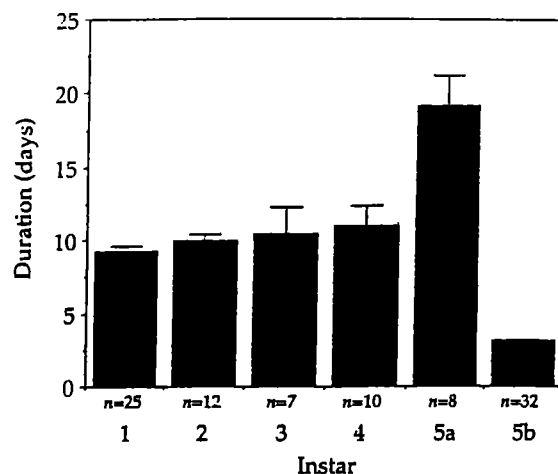


Fig. 4. Duration of nymphal life stages of *P. nr. bicincta* (stadia) including early (5a) and late (5b) 5th instars under greenhouse conditions. Bars are standard errors.

feeding sites. Spittlebugs were adept at moving over the litter and through the dense sward if outside the spittle mass. Although nymphs tended to move little over their life span, general observations suggested that the foraging range of 5th instars was ≈ 1 m. When forced to seek a new site, the older instars, at least, were able to produce a backfull of spittle that may have afforded them some protection while outside the spittle mass.

Stadia increased slightly with each molt until the 5th instar when developmental time doubled. Mean developmental time ($\pm$ SE) for instars 1–4 and 5a and 5b were 9.24 ± 0.40 , 9.94 ± 0.51 , 10.38 ± 1.86 , 10.95 ± 1.38 , 19.13 ± 2.08 , 3.08 ± 0.10 d, respectively (Fig. 4).

Adult Morphology. Both sexes of *P. nr. bicincta* had conspicuous coloration consisting of a crimson venter and a black dorsum punctuated by 3 transverse stripes crossing at the crest of the pronotum, the middle of the forewings, and at half the remaining distance to the posterior edge of the forewing (Fig. 5). Sexes were easily distinguished on the basis of genitalia, but color and size characters allowed sexing in the field without capture. Compared with males, females tended to have narrower forewing stripes and duller crimson markings combined with shorter and broader bodies, and wider head capsules (Table 1). Adults of both sexes had styli that were shorter than those of 5th instars.

Reproductive Biology. For females, the minimum time to 1st copulation ranged from 18–102 h (55.8 ± 7.62 , $n = 13$). Minimum estimates of time in copula were 0.25–40 h (12.4 ± 5.38 , $n = 8$). Because observations were only made every 1–3 h, the longer copula measurements may have failed to identify breaks in copulation. Observations of multiple copulations included 2 copulations over 2.5 and 5.0 d, and 3 copulations over 3.5, 6.0, and 7.0 d.

Minimum estimates of preoviposition period were 14.9–21.9 d (18.7 ± 0.92 , $n = 7$). From the few lon-



Fig. 5. Adult male (foreground) and female *P. nr. bicincta* in copula on East African star grass.

gevity observations completed ($n = 8$), adults lived 3.3–48 d on potted star grass in sleeve cages. One virgin female survived 57 d in a greenhouse on coastal Bermuda grass.

Females oviposited in the top layers of the soil near the base of their host plants. Most of the eggs laid in

the pots were recovered from the top 1.5 cm of soil; smaller proportions were recovered from greater depths in the soil, from the litter layer, and only a very few were attached to the plant itself (Fig. 6).

I estimated the oviposition rate of *P. nr. bicincta* females on various occasions under differing condi-

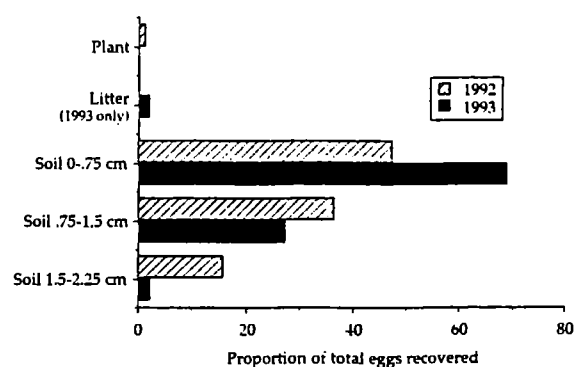


Fig. 6. Distribution of eggs of *P. nr. bicincta* laid on potted star grass with a bare (1992, $n = 716$) and litter-covered (1993, $n = 477$) soil surface.

tions (Peck 1996). Each estimate derived from the maximum number of eggs oviposited by a group of females over a 1-3-d period. Mean daily oviposition was 6.86 ± 0.57 eggs per female, with a range of 4.0-16.5 ($n = 25$).

Female *P. nr. bicincta* will copulate with both *P. simulans* and *P. plagiata* if these congeners are held in the same collecting jar. *P. simulans* males (immigrants) also commonly copulated with *P. nr. bicincta* in the field. There was no evidence to suggest that interspecific matings led to successful reproduction. No unusual *P. nr. bicincta* color morphs were observed, and 10 eggs from a *P. nr. bicincta* (female) and *P. simulans* (male) cross were not viable.

On star grass in the field and greenhouse, adults fed on all parts of the leaves and stems while positioned with the head facing upward. With the exception of 1 host, adults and nymphs chose to feed on grasses associated with pastures, roadsides, and forest edges (Table 2); *Ilex haberi* is a remarkable host in that it is a tree found in some pastures and is used exclusively by males (Peck 1998).

Oviposition Experiments. In the preference experiment, activity on the substrate was significantly affected by soil cover ($F = 6.610$, $P > F = 0.014$) but not fertilizer ($F = 0.288$, $P > F = 0.595$). More females were observed on litter substrates than on soil (Table 3). Activity on the plant was not significantly affected by soil cover ($F = 0.1470$, $P > F = 0.233$) or fertilizer level ($F = 1.757$, $P > F = 0.194$). Although very few eggs were recovered, the number of eggs laid per female was higher in bare versus litter-covered soil.

In the no-choice experiment, rate of oviposition increased with plant height and plant weight, decreased with increasing fertilizer, and was higher on pots with a litter layer rather than bare soil (Table 4). The number of eggs laid per female over the experimental period on litter and bare soil was 6.41 ± 1.12 and 3.36 ± 3.20 , respectively; on low, medium, and high fertilizer levels it was 6.39 ± 1.63 , 4.64 ± 1.13 , and 3.33 ± 0.87 , respectively. For females on litter substrate, fertilizer treatment had no effect on the proportion of eggs laid in the soil versus litter ($F = 1.94$,

Table 2. Host plants of *P. nr. bicincta*

Host family	Host plant	Life stage	
		Nymph	Adult
Aquifoliaceae	<i>Ilex haberi</i>		X ^a
	<i>Kyllinga brevifolia</i> Rottb	X	
Cyperaceae	<i>Kyllinga</i> sp. 2	X	
	<i>Cynodon nlemfuensis</i>	X	X
	<i>Digitaria abyssinica</i> Stapf	X	X
	<i>Hyparrhenia rufa</i> (Nees) Stapf	X	X
	<i>Ichnanthus nemorosus</i> (Swartz)		X ^b
	Doell		
	<i>Lasiacis</i> sp.		X ^b
	<i>Paspalum conjugatum</i> Bergius	X	X
	<i>Pennisetum clandestinum</i>	X	X
	<i>Pennisetum purpureum</i> Schum.	X	X
Poaceae	<i>Sporobolus</i> spp.	X	X
	"San Juan"	X	X
	"St. Augustine"	X	X

Nymphal observations are of spittle masses found on hosts in the field, where the species of each occupant was verified by rearing it to adult in the greenhouse. Adult observations are individuals feeding on hosts in the field and seen to pass exudate. Two Poaceae species were not determined and are listed by their common name.

^a Limited to adult males.

^b Observed in the laboratory only.

$P > F = 0.120$). The percentage of eggs in soil was 92.1, 77.2, and 87.0 for the low, medium, and high fertilizer treatments, respectively.

Discussion

Management Implications. The resolution upon which management decisions and advances depend is not attainable without an explicit analysis and consideration of the variation in the association between grassland spittlebug species, their life stages, and the pasture habitat.

Most population studies on cercopids do not distinguish among instars or sympatric species (Oomen 1975, Melo et al. 1984, Ramiro et al. 1984) and thereby lose the resolution of species-specific age structure necessary for accurate interpretation of local population dynamics. For *P. nr. bicincta*, 5 instars can be reliably distinguished on the basis of both morphological and behavioral characters. Overall size (particularly head capsule width), features of the compound eyes and wing pads, and characters of the spittle mass allow the determination of instar and might be useful in discriminating between co-occurring species. Five instars are confirmed for spittlebugs in the genus *Prosapia* (Pass and Reed 1965, Fagan and Kuitert 1969, Oomen 1975) and the rest of the Cercopidae, Clastopteridae, and Aphrophoridae (Weaver and King 1954, Arango and Calderón 1981, Kuenzi and Coppel 1985).

Young *P. nr. bicincta* nymphs are more particular in their choice of feeding sites than older nymphs. Therefore, the period between egg hatch and establishment of the 1st spittle mass may represent a vulnerable window exploitable by control tactics. Many factors known to play a role in feeding site and host-plant selection among cercopids could contribute to the

Table 3. Number of eggs recovered and observations of females on substrate and plants in preference experiment when offered a choice of low or high fertilizer levels, and bare or litter-covered soil

Treatment	Mean $\pm$ SE adults per observation		Mean $\pm$ SE eggs per female	n
	On substrate	On plant		
Substrate: soil	1.10 $\pm$ 0.22a	17.45 $\pm$ 2.49a	0.12 $\pm$ 0.04a	15
litter	2.31 $\pm$ 0.39b	17.40 $\pm$ 2.26a	0.04 $\pm$ 0.02b	15
Fertilizer: fertilized	1.77 $\pm$ 0.38a	19.73 $\pm$ 2.88a	0.07 $\pm$ 0.03a	15
not fertilized	1.63 $\pm$ 0.31a	15.12 $\pm$ 1.57a	0.09 $\pm$ 0.03a	15

limitations of earlier instars, including depth to xylem elements, tissue toughness, and unfavorable microclimate (Hoffman and McEvoy 1985, 1986; McEvoy 1986). In addition, sap at other plant sites may be too difficult to extract given xylem tension generally increases with distance from the roots (Raven 1983). Plant morphology may constrain feeding-site selection more than microclimate given that one-quarter of 1st instars were found on weedy hosts in microclimates more similar to nonroot portions of the plant.

Current control measures in Monteverde combine habitat management, through controlled grazing, with high inputs of fertilizer to promote vigorous regrowth of the sward. Despite a preference for laying eggs on bare soil, *P. nr. bicincta* oviposition rates are augmented by the presence of a litter layer. Spittlebug abundance may therefore be modified by grazing management practices because grazing pressure alters the habitat structure of pastures, including litter (Hewitt 1988). The presence of litter also increases oviposition in the froghoppers *Deois flavopicta* (Stål) and *Notozulia entreriana* (Berg) (Hewitt 1985). Although *P. nr. bicincta* did not select food plants or oviposition sites in response to recent addition of fertilizer, the nitrogen status of host plants plays an important role in the feeding and oviposition behavior of phytophagous insects. Examples from 2 extremes are nymphs of *Philaenus spumarius* (L.) that select feeding sites based on amino acid concentration (Horsfield 1977) and the superfamily's predilection for nitrogen-fixing host plants (Thompson 1994). Despite the unclear results from this study, the use of fertilizer to augment plant vigor and tolerance to pests should be weighed against potential increases in oviposition rates and attractiveness.

With the means to determine instar in the field, sampling programs will produce a detailed picture of current age structure to gauge developmental rates and time the application of control techniques. Over the extended period of nymphal development there

should be ample opportunity to apply controls to depress populations below economic thresholds. After eggs hatch, new nymphs may be vulnerable to enemies and desiccation as they seek out feeding sites that are limited to only a subset of the resources available to older instars. They may therefore be severely impacted by heavy grazing, mowing, and other habitat management practices directed at infested pastures. With site-specific information on precipitation and froghopper phenology, it may be possible to accurately predict the periods of hatching (King 1975). Finally, some forage grasses, such as *Andropogon gayanus* Kunth, achieve morphological resistance to spittlebugs because of a deep-rooting growth habit with few secondary roots available as feeding sites for early instars (Ferrufino and Lapointe 1989). But under field conditions, where pastures include a mix of secondary grasses and other herbs, 1st instars may find sufficient alternative feeding sites to surpass economic thresholds later in the generation.

Comparative Biology. New information from *P. nr. bicincta* expands our knowledge about variation among grassland cercopids. Compared with other *Prosapia* and other cercopids, *P. nr. bicincta* has an extended nymphal stage and preoviposition period (Table 5). Adults oviposit almost exclusively in the soil whereas *P. bicincta* and *P. plagiata* lay eggs in trash and litter, between the leaf sheath and the stem, and occasionally into the epidermis itself. A comparison of *Prosapia* with other grassland genera, such as the well-studied genus *Aeneolamia* (Guagliumi 1962, 1973; Fewkes 1969), suggests that there is more variation in biological and behavioral traits relevant to pest management between species of the same genus than between genera.

The construction of characteristic teneral spittle masses for molting of the ultimate instar to the adult appears to be a general behavior of *Prosapia* and the families Cercopidae and Aphrophoridae. Several authors have reported teneral spittle masses to be hollow, exceptionally high in the grass sward, or otherwise removed from typical feeding sites (Washbon 1968). It is reasonable to suggest that these spittle masses serve to protect the teneral adult until the exoskeleton has hardened, but it is unknown why 5th instars move so far to construct them and why they often do so in exposed positions where nymphs rarely feed. For example, I have noted teneral spittle masses of *Cephus siccifolius* Stål (Aphrophoridae) in the pasture sward below their host trees such as *Acnistus arborescens* Schlect. (Solanaceae). There may be ben-

Table 4. ANOVA (reduced model) of the number of eggs laid per female (square-root transformed) in groups held on pots with low, medium, and high fertilizer addition, and with bare soil or litter cover

Source	SS	df	F	P > F
Fertilizer level	3.761	2	2.902	0.0761
Soil cover	5.571	1	8.598	0.0077
Plant dry mass	2.915	1	4.498	0.0454
Plant height	2.615	1	4.036	0.0570
Error	14.256	22		

Table 5. Comparisons of oviposition sites and the duration of *Prosapia* life stages including nymphal and adult longevity, and prematuring and preoviposition period

Species	Duration: mean d (range)				Primary oviposition site	Reference
	Nymph	Adult	Premating	Preoviposition		
<i>P. nr. bicincta</i>	60 (43-75)	≤30			Behind leaf sheaths	Beck 1963 ^d
		23	(5-9)	(6-13)	Left litter	Byers 1965 ^d
	(34-60) ^b	≤42 ^a			Soil	Pass and Reed 1965
	50	21		7	Leaf litter	Fagan and Kuitert 1969 ^a
<i>P. plagiata</i>	(40-56)	≤25			Behind leaf sheaths	Washbon 1968 ^a
	58 ^c	(7-18) ^a	(3-4) ^a	(5-8) ^a	Epidermis	Picado 1970
<i>P. similans</i>	(22-48)					Velasco and Sifuentes 1970
	26					Oomen 1975 ^b
<i>P. nr. bicincta</i>	63 (34-98)	18 (3-48)	2.3 (0.75-4.25)	18.7 (14.9-21.9)	Soil	Peck, this study ^a

^a Studies were performed in the greenhouse.

^b Studies were performed in the field.

^c Studies were performed at 21.5-23°C, 69-85% RH.

^d Studies were performed at 23.5°C, 70% RH.

effits that balance the costs of traveling to a distal, more exposed site and investing energy in a new spittle mass. Perhaps nymphs are seeking out flat, horizontal surfaces for basal support of the hollow spittle mass. The family Clastopteridae may not share this behavior given reports of molting to the adult outside the spittle mass (Kuenzi and Coppel 1985).

Certain features of *P. nr. bicincta*'s habitat pose challenges to insect herbivores: a severe dry season, regular disturbances associated with grazing cattle, and abundant generalist predators. In overcoming this adversity, *P. nr. bicincta* has rallied defensive and protective devices associated with the domain of K-strategists. Eggs laid in the soil may gain protection from desiccation, mammalian herbivory, and ant predation during the dry-season months they endure while in diapause. Nymphs within spittle masses at the soil surface may profit from favorable microclimates, be defended against most invertebrate enemies, and avoid consumption by cows. Adults display warning colors that probably advertise their ability to bleed reflexively, as a deterrent (Peck 1996), and to jump as an escape. The ability of the life stages to defend and protect themselves allows pasture cercopids to achieve pest status despite the adversity of habitat and food resource, and it allows *P. nr. bicincta*, specifically, to achieve a pest status comparable with other grassland cercopids despite being the only known univoltine species of the group (Peck 1996).

Uncovering the details of *P. nr. bicincta*'s life style has expanded our knowledge of the variation in cercopid natural history. The results highlight how the associations of cercopids with grasslands vary in ways relevant to the refinement of management tactics, thereby confirming the need to discern differences—in addition to seeking generalities—among species in this pest complex.

Acknowledgments

I am grateful to Joe and Jean Stuckey, Stella Wallace, and the other people of Monteverde who lent their support to my 4 field seasons in their pastures and community; to Jacqueline Madrigal for assistance in the field over 2 seasons; to Richard

Root and Maurice Tauber for extensive comments on early drafts; and to 2 anonymous reviewers. Arthropod voucher specimens are deposited at the Cornell University Insect Collection under Lot #1227. This work was supported by grants from the Organization for Tropical Studies, Cornell Graduate School, Andrew W. Mellon Foundation, Cornell International Institute for Food, Agriculture and Development, Sigma Xi and the Mario Einaudi Center for International Studies at Cornell.

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Received for publication 18 February 1997; accepted 25 February 1998.

Seasonal Fluctuations and Phenology of *Prosapia* Spittlebugs (Homoptera: Cercopidae) in Upland Pastures of Costa Rica

DANIEL C. PECK¹

Department of Entomology and Section of Ecology and Systematics, Comstock Hall, Cornell University, Ithaca, NY 14853

Environ. Entomol. 28(3): 372-386 (1999)

ABSTRACT Seasonal fluctuations in *Prosapia* (Homoptera: Cercopidae) abundance were documented over 4 yr in 3 upland dairy pastures of Costa Rica. *P. nr bicincta* (Say) completed only 1 relatively long-lived generation each year between May and September. First instars appeared in May at the start of the wet season, progressed through 5 instars and peaked in abundance in mid-June. Densities as high as 277 spittlebugs per square meter were reached. Adult populations peaked late June to early July and achieved densities up to 260 froghoppers per 50 sweeps of an insect net. Distinct peaks of adult males generally occurred 3-4 wk in advance of the maturation of 5th instars and the principal adult peaks. Males outnumbered females 5.6:1 in sweep net surveys. Nymph and adult abundance fluctuated widely among paddock-years in no clear pattern with respect to paddock or predominant forage. Phenological analyses based on cumulative insect-days did not detect differences in population initiation or development rate across paddock-years. Teneral and adult males peaked earlier than their respective females (protandry). In 5 of 8 and 4 of 9 paddock-years, adult males and females, respectively, peaked in abundance before same sex tenerals, indicating colonization of local pastures. Additional evidence for immigration was the abrupt appearance of male *P. simulans* (Walker) at the same time in all paddocks each year. This species did not complete its life cycle in local pastures because females and nymphs were absent from surveys. Explorations of pastures at varying elevation and distance from survey paddocks demonstrated that within 10 km *P. nr bicincta* populations matured 2.5 wk earlier. Adults derived from those populations may become available as colonists to local pastures. The nearest breeding populations of *P. simulans* to sites where males were recovered were 485 m lower in elevation and 3.4 km distant.

KEY WORDS *Prosapia nr bicincta*, *Prosapia simulans*, dispersal, population dynamics

SPITTLEBUGS AND FROGHOPPERS are the most injurious and widespread pests of forage grasses in the New World tropics and subtropics. Their rise in pest status has paralleled the introduction and broad establishment of productive African grasses (e.g., Enkerlin and Morales 1979). Adults induce a phytotoxemia in susceptible grasses (Byers and Wells 1966, Valério et al. 1988) that causes "froghopper burn" and leads to a decrease in nutritive value, palatability, and productivity (Fagan and Picado 1971, Barrientos et al. 1988, Valério and Nakano 1988). Nymphs contribute to water stress and decreased productivity (Silva 1982, Barrientos et al. 1988). Both life stages thereby inhibit the establishment and persistence of improved grass varieties (Taliaferro et al. 1967, Valério and Nakano 1987, Lapointe et al. 1992) and limit the production of milk and beef cattle on rangelands and pastures throughout their range.

Cercopid nymphs, or spittlebugs, reside in the protection of masses of spittle that they construct to surround themselves at feeding sites on host plants. Adults, or froghoppers, do not produce spittle; they

rely instead on jumping ability and warning coloration (Peck 1996) for defense as they hop, flit, and fly about the pasture sward on the same host grasses. Both life stages feed on xylem sap of their host plants (Hagley 1965, Byers and Wells 1966, Marshall and Cheung 1975), which include other prominent graminaceous crops such as sugar cane, *Saccharum officinarum* (L.); rice, *Oryza sativa* (L.); and turfgrass (Fewkes 1969, Guagliumi 1973, Nilakhe 1985, Tashiro 1987).

This pest complex is taxonomically diverse, comprising 7 genera from the family Cercopidae (sensu Metcalf 1961): *Aeneolamia*, *Deois*, *Mahanarva*, *Notozulia*, *Prosapia*, *Sphenorhina*, and *Zulia*. *Prosapia* is the northernmost genus, ranging from southern Ontario to Panama (Hamilton 1977, 1982). In Costa Rica, 9 species from 3 genera have now been identified as economically important on forage grasses and sugar cane: *A. albofasciata* (Lallemand), *A. lepidior* (Fowler), *A. postica* (Walker), *A. reducta* (Lallemand), *P. nr bicincta*, *P. plagiata* (Distant), *P. nr plagiata*, *P. simulans* (Walker), and *Z. vilior* (Fowler) (Thompson 1996). Notable host plants in Costa Rica include *Brachiaria decumbens* Stapf; coastal Bermuda grass, *Cynodon dactylon* L.; East African star grass, *Cynodon nlemfuensis* Vanderyst; kikuyu grass, *Pennisetum clan-*

¹ Current address: International Center for Tropical Agriculture, A.A. 8713, Cali, Colombia.

destinum Hochst.; and pangola grass, *Digitaria decumbens* Stent (Washbon 1968, Fagan and Picado 1971, Peck 1998a).

Outbreaks of cercopids in Costa Rican pastures were first reported in the late 1940s (Picado 1970, Fagan and Picado 1971). In the upland region of Monteverde (Puntarenas Province), damage from these native insects in the late 1950s forced a conversion from the highly susceptible kikuyu grass to the partially tolerant East African star grass. The severe infestations might have brought an end to the young dairy industry if not for the widespread introduction of star grass (Peck 1999). Despite the change in forage, farmers still endure severe cercopid problems because control techniques have largely failed to suppress populations. Although tolerant to cercopid feeding, star grass is visibly impacted by high insect densities, which inflict water stress and decreased productivity if not severe phytotoxemia.

There are 3 reasons why producers of the region are prevented from maintaining preferred kikuyu grass pastures and are unable to limit production losses imposed by high cercopid populations. First, producers lack basic information on pest status because quantitative studies addressing the impact of cercopids on star grass have not been performed. Second, the appropriateness and effectiveness of the most widespread control strategy (in Monteverde) have not been tested. This strategy combines heavy grazing, for full utilization of forage resources, with regular applications of chemical fertilizer, to promote vigorous regrowth. Finally, the biology and behavior of the most abundant species have not been considered in the development and application of control programs.

Management of these pests, in general, is compromised by a failure to recognize that the nature of spittlebug impact may vary tremendously across their range. Given the taxonomic diversity of the group and the range of habitats they inhabit—a product of geographic range, climatic factors, elevation, and pasture management—there is a clear need for delineating the differences, rather than similarities, within this complex. We do not possess the detailed, site-specific understanding in which to firmly ground effective individual control techniques, much less integrated pest management (IPM).

Studies on the agricultural ecology of *Prosapia* in Monteverde were carried out to fill the gap in understanding of the principal pest species, a currently undescribed species of *Prosapia* closely related to *P. bicincta* (Say) (hereafter designated *P. nr bicincta*). Over a 4-yr period, I made detailed censuses to track the population dynamics of *P. nr bicincta* nymphal and adult life stages. Few other population surveys have lasted >2 yr, few have occurred in intensive rather than extensive grazing systems, and none has distinguished among all nymphal and adult life stages. This report addresses the population dynamics of *P. nr bicincta*; it focuses on the on-farm and yearly variation in seasonal abundance and phenology and gathers evidence for long-distance dispersal capabilities. The implications of this long-term (4 yr), detailed (assess-

Table 1. Seasonal precipitation in Monteverde over 4 survey years

Month	Year			
	1991	1992	1993	1994
Jan.	21.1	31.8	74.7	24.5
Feb.	71.6	59.9	29.6	21.3
Mar.	22.6	42.7	81.4	25.9
April	16.0	61.8	32.7	114.6
May	357.6	102.6	607.7	71.3
June	326.9	367.8	328.3	118.1
July	306.6	340.0	203.4	175.2
Aug.	302.6	203.3	419.1	273.1
Sept.	270.5	330.7	333.8	241.0
Oct.	404.6	252.2	263.3	412.2
Nov.	103.4	170.1	90.3	292.4
Dec.	166.7	289.3	59.2	203.6
Total	2,370.2	2,252.2	2,523.5	1,973.2

Rainfall data were collected by J. Campbell at 1,540m and ~4 km from survey sites.

ment of all nymphal and adult life stages) study for improving the management of grassland cercopids is discussed.

Materials and Methods

Site Description. Investigations were carried out in the dairy producing region of Monteverde, Puntarenas Province, Costa Rica. This is a seasonally wet area in the Tilarán Mountains where the landscape is a mix of pastures and forest, 1,300–1,600 m elevation, 10°18' N, 84°48' W. Mean yearly precipitation from 1991 to 1994 was 2,280 mm with 78% falling during the wet season months of May to October (Table 1). Dairy pastures of the zone are typically managed under intensive rotational grazing; cows move in herds from 1 paddock to the next every half day or few days, returning to the same paddock after the grass has regrown (Griffith et al. 1999).

Cows share pastures of this zone with a complex of 4 grassland cercopids: *Aeneolamia postica*, *Prosapia plagiata*, *P. simulans*, and the most abundant species *P. nr bicincta*. These species construct spittle masses at or near the soil surface on grass stems and surface roots. Like all grassland spittlebugs, nymphs pass through 5 instars. Both nymphs and adults feed on a subset of the herbaceous plants associated with pasture habitats, predominantly forage grasses (Peck 1998a).

Survey Paddocks. Seasonal fluctuations in all nymphal and adult life stages were followed in 3 pasture paddocks (1,340–1,360 m elevation) located on a single farm. Each survey paddock (0.19–0.21 ha) was managed under the regular system of intensive rotational grazing, in this case ~40 cows for 4 h every 2–3 wk. The plant composition of paddocks C2 and S2 was primarily star grass, or "estrella" (90 and 85%, respectively), interspersed with the clump grass "pitilla" (*Sporobolus* spp.; 5%) and other weedy herbaceous species (5 and 10%, respectively). Paddock S1 was largely composed of kikuyu grass (65%) with some star grass (30%) and other nonforage herbs and grasses (5%) (Peck 1996). Paddock C2 was centrally situated

distant; and site 3 was at 1,160 m elevation, 2.1 km distant.

Results

The 4 species of pasture froghoppers were easily distinguished in the field without magnification by using color and size characters. *A. postica* was the smallest of the 4 species, black, with red markings consisting of 2 transverse dorsal bands on the elytra and a V-shaped stripe on the posterior edge of the scutellum. *P. nr bicincta* was the largest, also with red markings on black, but the most anterior band was straight across the crest of the pronotum. The head and venter were crimson. *P. simulans* was slightly smaller than *P. nr bicincta*, yellow replaced the red, and the transverse lines were occasionally abbreviated or reduced (particularly in females). Sometimes the head and venter were pink (22%, $n = 900$). *P. plagiata* was slightly smaller than *P. simulans*, with a light brown dorsum and dark brown venter. Approximately 8% ($n = 727$) of individuals had the brown replaced by red. The sex of all 4 species was easily determined by viewing the adult genitalia.

All nymphs in the 3 survey paddocks were assumed to be *P. nr bicincta* because teneral adults of other species were never extracted from spittle masses. Considering the total number of teneral adults observed in population counts ($n = 209$), nymphal populations of other grassland species therefore comprised <0.48% of the total. This indicates that only *P. nr bicincta* completed its life cycle in the survey paddocks, although adults of other species were occasionally encountered. *A. postica*, *P. plagiata*, and *P. simulans* adults all appeared in surveys at some point, but their contribution to the overall numbers of froghoppers collected each season was usually small, ranging from 2.1 to 17.3% (C2), 4.7–20.3% (S1), and 1.7–16.2% (S2). The following abundance results pertain only to *P. nr bicincta*.

Nymph Abundance. Nymph abundance peaked in mid-June. Over all 4 yr the dates of peak abundance of total nymphs (50% cumulative insect-days, excluding teneral adults) ranged from 9 to 23 June (C2), 30 May–21 June (S1), and 17 June–8 July (S2). Maximum density of nymphs per square meter varied from 62 to 277 (C2), 100 to 154 (S1), and 46 to 200 (S2) (calculated from counts in single quadrats). Abundance curves show the progression through the 5 instars and teneral adult stage as the brood matured (Figs. 1 and 2).

The appearance of 1st instars coincided with the return of the wet season rains in May (Table 1). After surviving the dry season as diapausing eggs in the soil, 1st instars establish spittle masses on the surface roots and fine stems of grasses and sedges (Peck 1998a). This nymphal stage was the most difficult to detect given the small size of the spittle masses and the preference for soil surface (and likely subsurface) and litter layer microhabitats. Over all 4 yr the earliest detection of 1st instars varied considerably, from 7 May to 12 June (C2), 11 May to 2 June (S1), and 7 May to 2 June (S2) (Figs. 1 and 2). Although there were pronounced

emergence peaks at the beginning of the season, 1st instars appeared in surveys as late as 11 July (C2), 8 June (S1), and 27 June (S2).

Later instars were increasingly easy to find although still limited largely to the litter layer and soil surface. A wider range of feeding sites are available to older nymphs, including stolons, mature stems, and sometimes sites several centimeters into the canopy (Peck 1998a). Teneral adults, still encountered inside spittle masses, marked the earliest date of maturation of local populations. The 1st detection of teneral adults varied from 15 May to 27 June (C2), 18 May to 30 June (S1), and 15 June to 21 July (S2) (Figs. 1 and 2). Much of this extreme variation may be attributed to small sample size, given that teneral adults reside in spittle masses less than a day and were therefore less likely to be sampled.

Differences in abundance among instars reflected varying degrees of conspicuousness and duration in the field. The change in the abundance curves from 5th instars to teneral adults, for instance, does not indicate high mortality between the 2 life stages; rather it reflects their respective long and short duration in the field.

Adult Abundance. The largest adult abundance peaks occurred between late June and early July. Over all 4 yr the dates of peak abundance of adult males (50% cumulative insect-days) ranged from 22 June to 1 July (C2), 21 to 29 June (S1), and 24 June to 10 July (S2); adult females peaked in abundance from 27 June to 15 July (C2), 27 June to 11 July (S1), and 11 to 30 July (S2). Maximum abundance of total male and female froghoppers varied from 40 to 260 (C2), 57 to 146 (S1), and 21 to 139 (S2) individuals per 50 sweeps.

Over all 4 yr the earliest appearance of adults in sweep net surveys varied from 7 May to 2 June (C2), 7 to 30 May (S1), and 11 May to 2 June (S2) for males, 7 May to 26 June (C2), 11 to 30 May (S1), and 25 May to 14 June (S2) for females (Fig. 3). In every year but 1992, however, there were distinct early season adult male peaks that occurred 3–4 wk before the principal adult peaks and significantly broadened the period of adult presence. These early peaks appeared at about the same time across all 3 paddocks any particular year. In addition, the shape of the abundance curves among paddocks within any 1 yr appeared to be more similar for males than for females.

Far more males than females were collected in pastures during sweep net surveys. The overall ratio of males to females calculated over the 4 yr was 5.60, and within the 3 paddocks it varied from 3.10 to 5.62 (C2), 5.41 to 16.47 (S1), and 5.90 to 7.71 (S2). These high relative numbers of males to females probably do not accurately reflect true proportions in the field because females oviposit in the soil (Peck 1998) where they are less likely to be censused by sweep net.

Comparative Abundance. Nymph abundance was compared between years and sites using 4th-instar cumulative insect-days. Over the 4 yr of this study, this relative measure of population size ranged from 210.5 (S2 1992) to 2,567.5 (C2 1994) insect-days, a 12.2-fold difference in abundance (compared with a 10.4-fold

mong 19 similar paddocks completely surrounded by forest. S1 and S2 were each bordered by other pastures and separated from each other by 30 m of windbreak and old pasture. C2 was ≈ 500 m distant, separated by forest and other pastures.

Sampling Procedures. Population counts of nymphs and adults were carried out approximately twice weekly over the wet season months of 4 consecutive years: 30 May–16 August (1991), 20 May–18 August (1992), 7 May–25 September (1993), and 7 May–9 August (1994). Each paddock was divided into 4 sections to facilitate sampling of cercopid life stages.

To census nymphs, I sampled each of the 4 sections with 1 (1991) or 2 (1992–1994) 0.25-m² quadrats randomly situated in the sward. A 1-m border along fence lines was not included. Quadrats were square in 1991, but rectangular (0.81 by 0.31 m) in subsequent years for greater ease of searching. Occupants were collected from all spittle masses within the quadrat that could be located in the litter and in the sward above the soil. The instar of each nymph was determined either in the field or under a dissecting scope after storage in 70% ethyl alcohol (using morphological features described in Peck 1998a). Teneral adults were also enumerated; this life stage spends a few hours in a specially constructed cave-like spittle mass that affords protection while the exoskeleton hardens (Peck 1998a). These data provided a measure of the absolute abundance of spittle mass occupants.

To census adults, I made 50 sweeps of an insect net (40 cm diameter hoop, 90 cm pole) in a haphazard zigzag fashion in each section between 1000 and 1200 hours (between the drying of morning dew and arrival of afternoon rains). This consistent sampling period controlled for biases in the number of sweepable adults that depend on the time of day (Nilakhe et al. 1987). If censuses coincided with rain or with cows grazing the paddock, surveys were delayed 1 d. The sex and species of each individual was noted to provide a measure of relative abundance. Adult voucher specimens were deposited at the Cornell Insect Museum under Lot #1227.

Population Analyses. Population curves were constructed by plotting Julian date against the sum of the counts in the 4 sections: nymphs per square meter and adults per 200 sweeps. Because the total number of surveys performed over the season varied between paddocks, seasonal insect abundance could not be compared directly between sites using the measure of total insects captured. To account for this and to facilitate phenological interpretations, I constructed phenograms based on calculations of cumulative insect-days, a measure of abundance, or population size, equaling the area under the population curves (Ruppel 1983). The peak abundance of life stages was designated as 50% cumulative insect-days (i.e., the date when half of the individuals of that life stage had appeared in the field).

All statistical analyses were performed by using the JMP statistical package, version 3.1 (SAS Institute 1989), with paddock-year as the unit of replication. To evaluate the effect of paddock and year on the abun-

dance of nymphs and adults, two-factor analysis of variance (ANOVA) was performed. Abundance was measured in cumulative insect-days. The comparison of nymphal abundance between sites and years was limited to the 4th instar because the occurrence of this nymphal stage was the least truncated by the actual sampling period and because the large spittle masses of this life stage should have been equally detectable across paddocks. Because the occurrence of adults in the field was truncated by the survey period more often than not, cumulative insect-days was calculated for the period 30 May–15 August, set by the briefest survey season (1991).

For the phenological analysis, a two-sided paired *t*-test was used to compare dates of peak abundance of 5th instars, teners, and adults. To assess the effect of paddock and year on population initiation and development rate, two-way ANOVA was performed on the *y*-intercept and slope derived from linear regression models for 50% cumulative insect-days on life stage (instars 1–5 and teneral adults).

Planned post-ANOVA orthogonal contrasts were used to test for differences between the kikuyu grass pasture (S1) and the star grass pastures (C2, S2) in abundance (4th instars and adults), development rate, and initiation date.

Regional Surveys. To gauge the variation in regional phenology of *P. nr bicincta* and *P. simulans*, 2 supplemental population counts were carried out at varying elevations in other zones of the Monteverde region. The 1st survey focused on distant sites northeast to northwest of survey paddocks where *P. nr bicincta* was also reported to be the principal pest species. Population counts of nymphs were made on 1 date (30 May 1994) about the time of peak spittlebug populations in local survey paddocks. Three pastures of predominantly East African star grass were chosen at the following elevations and distances from the local paddocks: site 1 was at 1,335 m elevation, 9.0 km distant; site 2 at 1,500 m elevation, 4.6 km distant; and site 3 was at 1,600 m elevation, 4.3 km distant. Census methods were identical to those for the local paddocks. This one-time sampling of nymphs allowed a comparison of development profiles (i.e., the proportion of the population in each instar) between Monteverde populations in survey paddocks surveyed the same day, and these distant survey sites. Adults were censused on a different date (14 July 1994) at 14 pasture sites. Sites ranged from 1,090 to 1,600 m elevation, and 3.8–9.4 km distant; 3 of them were the nymph sites surveyed above. Counts consisted of 25 sweeps with an insect net in each quarter pasture between 0900 and 1330 hours.

The 2nd survey comprised 3 lower elevation sites in the San Luis valley below the local survey paddocks. These explorations aimed to identify *P. simulans* breeding grounds through nymph and adult surveys on 4 dates in 1994 (26 May and 3, 10, 21 June). The methods of spittle mass counts and sweep net surveys were identical to local survey paddocks. Site 1 was at 1,090 m elevation, and 0.9 km distant from the local survey paddocks; site 2 was at 965 m elevation, 1.9 km

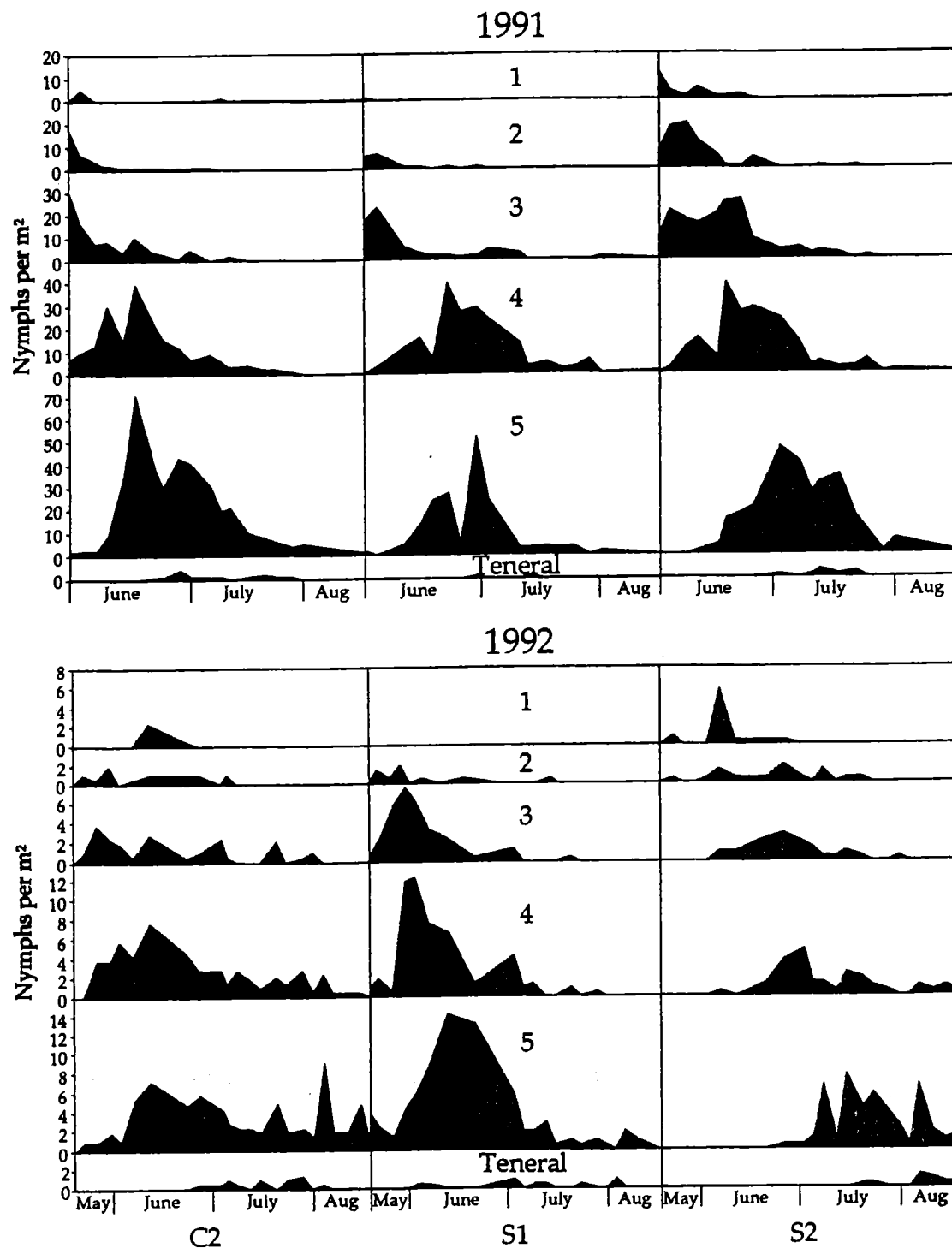


Fig. 1. Abundance curves for 5 nymphal instars (1-5) and teneral adults (*P. nr bicincta*) captured in spittle mass surveys in 3 paddocks (C2, S1, S2) over 1991 and 1992. The entire sampling season is depicted.

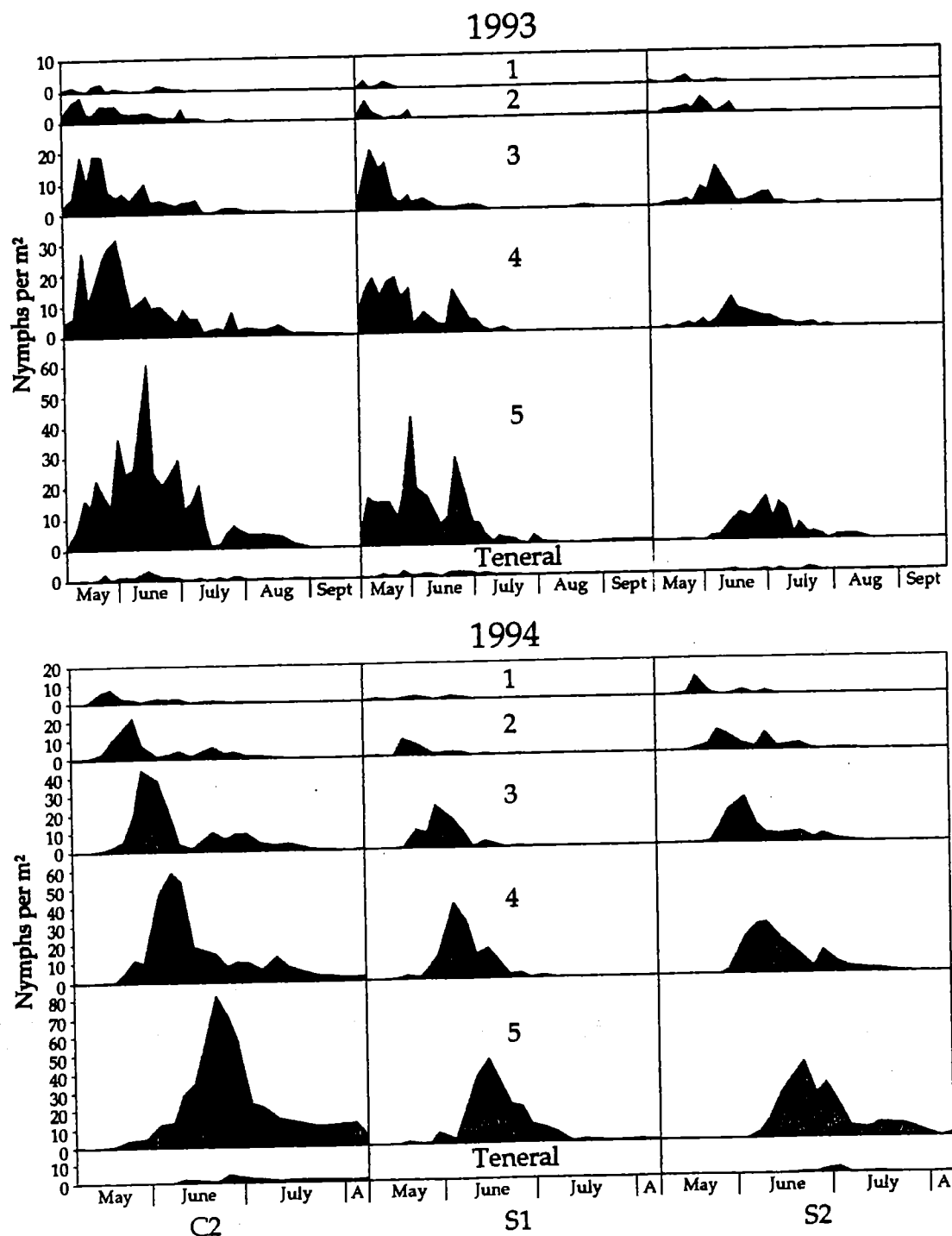


Fig. 2. Abundance curves for 5 nymphal instars (1-5) and teneral adults (*P. nr bicincta*) captured in spittle mass surveys in 3 paddocks (C2, S1, S2) over 1993 and 1994. The entire sampling season is depicted.

difference for all instars combined) (Fig. 4). Within each paddock, abundance varied 4.8- (C2), 2.4- (S1), and 7.5-fold (S2) over the 4 study years.

Fourth-instar abundance differed among paddocks ($F = 11.058$; $df = 2, 42$; $P < 0.0001$) and years ($F = 11.197$; $df = 3, 42$; $P < 0.0001$). There was no difference

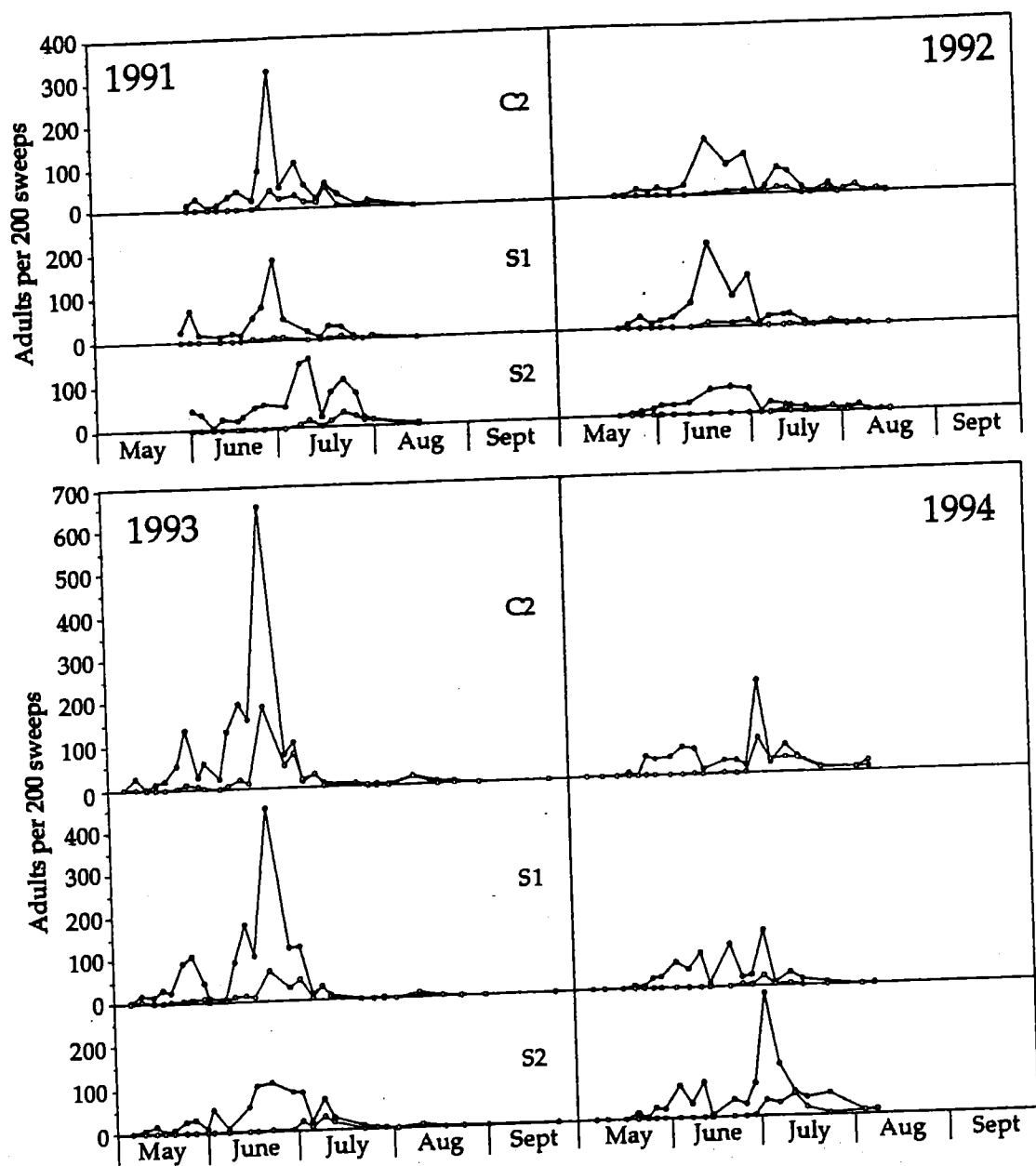


Fig. 3. Abundance curves for adult *P. nr bicincta* captured in sweep net surveys in 3 paddocks (C2, S1, S2) over 4 yr. The entire sampling season is depicted. Closed circles represent males, open circles females.

in abundance, however, between the kikuyu grass pasture (S1) and the star grass pastures (C2, S2) ($F = 0.065$, $df = 1$). There were no other apparent trends in the abundance differences between paddocks. The most extreme values were in C2 during 1993 and 1994 when abundance of 4th instars was about twice that of S1 and S2 (Fig. 4).

Adult abundance was compared between years and sites using total adult cumulative insect-days (male and female). Over the 4 yr of this study, this measure

ranged from 2,119.5 (S2 1992) to 9,668.5 (C2 1993), a 4.6-fold difference in abundance (Fig. 4). Within each paddock abundance varied 2.9- (C2), 2.7- (S1), and 2.4-fold (S2).

Total adult abundance differed among paddocks ($F = 4.546$; $df = 2, 42$; $P = 0.016$) and years ($F = 11.716$; $df = 3, 42$; $P < 0.0001$); however, no difference between the kikuyu star grass pastures was detected ($F = 0.223$, $df = 1$). As with the nymphs, there was no clear pattern to adult abundance differences between paddocks. Ex-

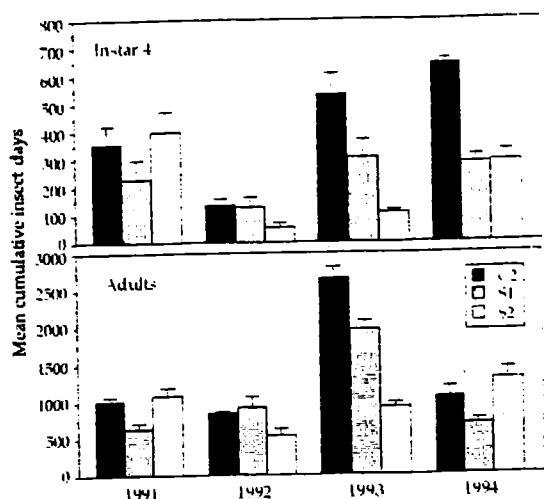


Fig. 4. Comparative abundance of 4th instars and total (male and female) adult *P. nr bicincta* in 3 paddocks (C2, S1, S2) over 4 yr. Cercopid abundance is measured as the mean cumulative insect-days calculated from the 4 sections in each survey paddock. Bars represent standard errors.

treme values occurred in 1993 where both C2 and S1 had very high populations. In the remaining years, overall abundance extremes varied only 2.4-fold (Fig. 4).

Phenology of *P. nr bicincta*. Phenograms of data expressed in cumulative insect-days showed a clear progression through the 5 nymphal instars in each of the 3 survey paddocks (Fig. 5). Recruitment from one life stage to the next as the population developed was reflected in the sequential dates of appearance of maximum abundance of 1st through 5th instars and teneral adults. Teneral adults represented the earliest appearance of adult froghoppers that derived from the maturation of local populations. Population synchrony includes both sequential recruitment and narrow period of peak abundance, which was expressed by the number of days between 30 and 70% cumulative insect-days and was represented graphically by the length of the thick bars in the phenograms (Fig. 5). The synchrony of resident populations was relatively highest in all paddocks of 1991 and 1994, and in S2 1992 and 1993.

When the adult data were superimposed on the nymphal phenograms, however, the recruitment pattern broke down. In 1991, adult females followed in progression from nymphal life stages, but adult males arrived at peak abundance (50% cumulative insect-days) in advance of teneral adults in all 3 survey paddocks (Fig. 5). Adult males reached 50% cumulative insect-days 1 July (C2), 29 June (S1), and 10 July (S2), 4–5 d earlier in each paddock than teneral adults, which peaked 6 July, 3 July, and 15 July, respectively. Adult males appeared significantly earlier than total teneral adults ($P = 0.003$, $df = 2$), at about the same time as 5th instars ($P = 0.156$, $df = 2$). Therefore, the majority of adult males captured in sweep net surveys appeared in the paddocks before the maturation of local nymph

populations. Two explanations for these data exist: either male *P. nr bicincta* developed and emerged as adults earlier than females (protandry) or adult males were colonizing survey paddocks from elsewhere.

To discover the reason for premature appearance of adult males, the sex of teneral adults was noted in spittle mass surveys of the 3 subsequent years. In 6 of 8 paddock-years from 1992 to 1994 (no male teneral adults were encountered in S2 1992), teneral males peaked in abundance before teneral females (Fig. 5), a significant difference ($P = 0.009$, $df = 7$). Adult males (from sweep net surveys) also peaked before adult females in 12 of 12 paddock-years from 1991 to 1994, a significant difference ($P < 0.0001$, $df = 11$). These data indicate that *P. nr bicincta* was protandrous.

In support of colonization, adult males peaked in abundance before teneral males 5 of 8 times (C2, S1 1992; S2 1993; C2, S1 1994), and adult females peaked before teneral females 4 of 9 times (C2, S1, S2 1992; S2 1993) (Fig. 5). This was not a trend over all paddock-years because adult male and female arrival was not statistically different from teneral adults of the same sex (males, $P = 0.984$, $df = 7$; females, $P = 0.772$, $df = 8$). However, these data indicate that there were occasions when a significant proportion of adults, particularly males, arrived earlier than expected had they derived from resident populations. In tandem with premature adult peaks (Fig. 3), these data offer clear indirect evidence for colonization.

No differences in population initiation or development rate were detected across paddocks and years. A linear regression model of 50% cumulative insect-days on nymphal and teneral life stages (6 observations) fit the data well across paddock-years (mean $R^2 = 0.9102$; range, 0.7120–0.9977). ANOVA on the y-intercept and slope of the regression lines did not detect differences between years or paddocks (Table 2). There was no difference in y-intercept or slope between the kikuyu and star grass pastures ($F = 0.0808$, 0.2873, respectively; $df = 1$).

Appearance of *P. simulans*. *Prosapia simulans* made up 5.3% ($n = 694$) of adult froghoppers collected in surveys over 4 yr. Of these, only 3 were adult females. No other females were ever seen in the survey paddocks or their vicinity in other explorations. Late 5th instar (earlier instars could not be identified to species) and teneral adult *P. simulans* were absent from spittle mass surveys. These observations indicate that *P. simulans* did not complete its life cycle in the local area.

Numerous adult male *P. simulans* were captured in sweep net surveys in late June and early July during discrete abundance peaks (Fig. 6). Population densities peaked as high as 100 individuals per 200 sweeps. *P. simulans* peaks coincided with the largest *P. nr bicincta* peaks (late June to early July), but the period of abundance was much more abbreviated and distinct. One major peak appeared in each paddock 1991–1993, whereas appearance was roughly bimodal in all paddocks in 1994. These males also appeared at nearly the same time across all paddocks in any 1 yr. Dates of peak abundance, as measured by 50% cumulative in-

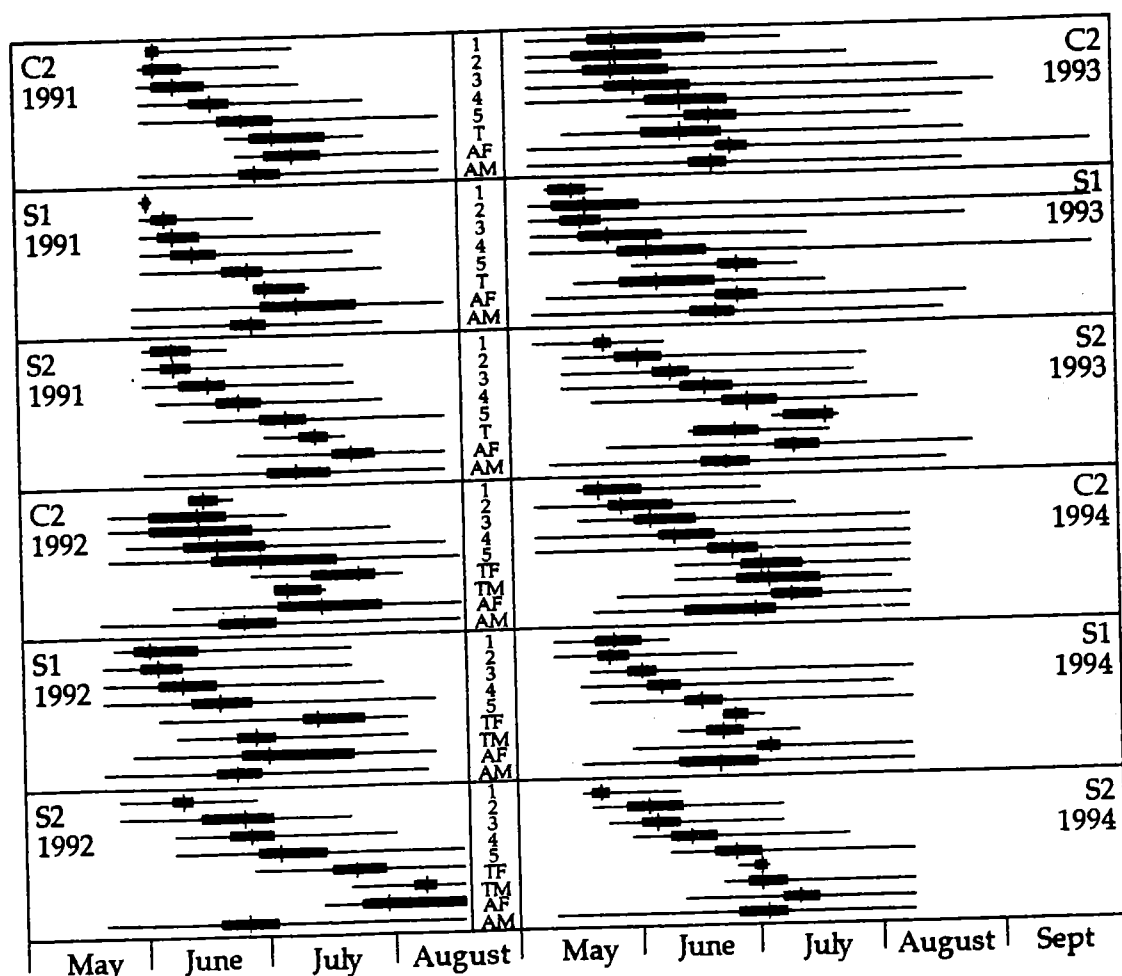


Fig. 5. Phenograms of *P. nr bicincta* life stages (instars 1-5, and teneral and adults by sex TF, TM, AF, AM) in 3 survey paddocks (C2, S1, S2) over 4 yr. Population data are expressed in terms of cumulative insect-days. Horizontal lines connect the 1st and last detection of each life stage during the survey season. Thick bars represent the period of 30-70% cumulative insect-days, and vertical lines represent the date of 50% cumulative insect-days, or peak abundance. Sex of teneral adults was not determined in 1991.

sect-days, varied very little from paddock to paddock: 27-30 June in 1991, 30 June-1 July in 1992, 20-24 June 1993 and 15-24 June 1994.

Table 2. ANOVA for linear regression parameters (y-intercept and slope) across paddocks and years

Source	df	SS	F	P > F
Y-intercept				
Paddock	2	148.25	2.269	0.1846
Year	3	436.69	4.456	0.0569
Error	6	196.00	32.667	
Slope				
Paddock	2	15.91	4.215	0.0719
Year	3	7.37	1.301	0.3574
Error	6	11.33	1.888	

Regression lines were calculated for each of 12 paddock-years with 6 life stages (x) and 50% cumulative insect-days (y).

Regional Surveys. There was considerable variation in the phenology of *P. nr bicincta* across the Monteverde region. Nymph populations of *P. nr bicincta* surveyed at distant high elevation sites (1st supplemental survey) were much more advanced than survey populations censused the same day, 30 May 1994 (chi-square test; $\chi^2 = 427.19$, $df = 3$, $P < 0.001$) (Fig. 7). Although 3rd instars were most represented in local paddocks, 5th instars predominated at the distant sites. Calculated as the mean time from 3rd to 5th instar, 50% cumulative insect-days ($n = 12$ paddock-years), spittlebug populations in Monteverde were ≈ 18.5 d behind those in pastures of the same or higher elevation 4-10 km distant.

Adults were captured in surveys at 13 of 14 sites. *P. nr bicincta* accounted for 69.1% of all froghoppers caught on 14 July 1994 ($n = 294$), *P. simulans* 1.0%, *P. plagiata* 29.6%, and *Aeneolamia postica* 0.3%. When adults were grouped

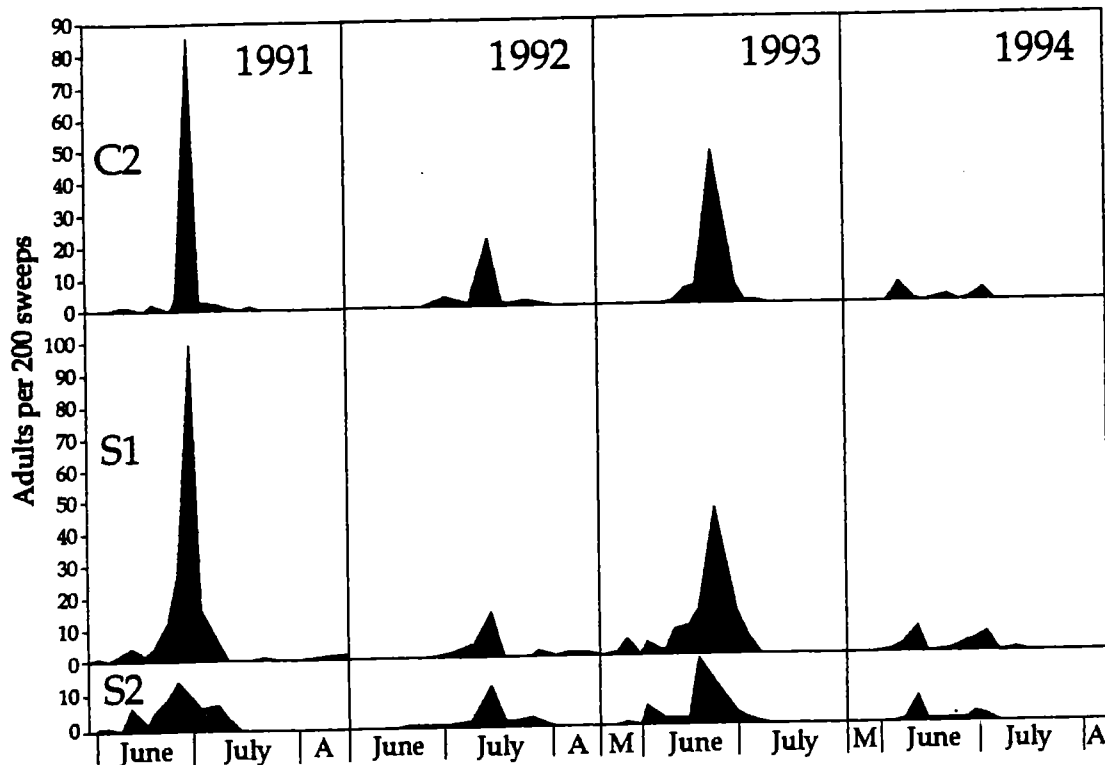


Fig. 6. Abundance curves of adult male *P. simulans* in 3 survey paddocks over 4 yr. Only the period of the survey season when *P. simulans* was detected is depicted.

into 3 elevation classes, <1,300 (4 sites), 1,300–1,499 (5 sites), and >1,500 m elevation (4 sites), *P. nr bicincta* comprised 92.2, 92.6, and 46.3% of total adults, respectively; *P. simulans* 5.9, 0.0, and 0.0%; and *P. plagiata* 0.0, 7.4, and 53.7%. *P. nr bicincta* was therefore relatively most abundant at low and mid elevation sites; *P. simulans* at low elevation sites; and *P. plagiata* at high elevation sites.

Explorations of lower elevation sites (2nd supplemental survey) revealed breeding grounds of *P. simulans* only in site 2. Early and late 5th instars of both *P. nr bicincta* and *P. simulans* were identified in spittle mass surveys ($n = 48$ spittle mass occupants) at this site; the latter were reared to the adult stage in the laboratory to verify the determination. Two adult male *P. simulans* were caught in sweep net surveys (3 and 21 June) ($n = 6$ total froghoppers). On other occasions, not part of the formal surveys, both male and female teneral *P. simulans* were taken from spittle masses of the same paddock, and adults of both sexes were caught with a sweep net. Spittle mass surveys in sites 1 and 3 yielded only *P. nr bicincta* ($n = 189$ spittle mass occupants); *P. simulans* nymphs and teneral adults were absent. Sweep net surveys yielded adult male and female *P. nr bicincta* but only 2 male *P. simulans* ($n = 24$ total froghoppers). Sites 1 and 3 therefore did not maintain breeding populations of *P. simulans*. The closest known site of teneral and adult females of this species was site 2, which is 1.9 km

distant from survey paddocks and 375 m lower in elevation.

Because of the presence of *P. simulans* in site 2, nymphs from that pasture were excluded from analysis of *P. nr bicincta*'s development profile (Fig. 7). In combined sites 1 and 3 for the dates 26 May and 3 June, 4th instars were most represented. *P. nr bicincta* nymph populations were therefore more advanced in San Luis than in Monteverde (chi-square test; $\chi^2 = 44.99$, $df = 3$, $P < 0.001$), indicating considerable variation in phenology within only 2 km of survey paddocks.

Discussion

Four years of population studies demonstrated that only 1 relatively long-lived generation of *P. nr bicincta* occurs in the Monteverde region of Costa Rica over the primary wet season months of May through September, despite apparently ample time for completion of a 2nd generation (in terms of seasonal rainfall). These conclusions are corroborated by studies that have shown this species to lay only diapausing eggs (Peck 1996). This is the 1st documentation of univoltinism in any neotropical grassland cercopid. *P. bicincta* and *P. simulans* complete 2 generations a year in Florida (Byers 1965) and Mexico (Oomen 1975), respectively. *P. plagiata* (= *P. distantii*) completes 3

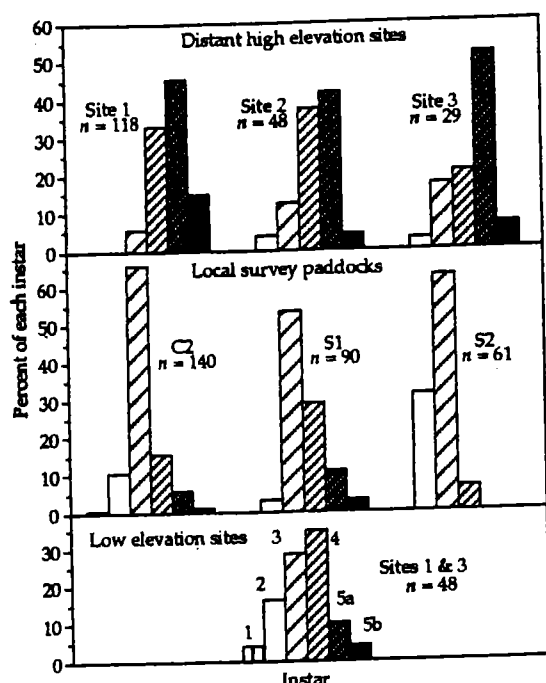


Fig. 7. Development profiles of *P. nr bicincta* nymph populations. Fifth instars are separated into early (5a) and late (5b) stages that are morphologically distinguishable. Distant, high elevation sites of the 1st supplemental survey (4.3–9.0 km from local paddocks) and local paddocks were surveyed 30 May 1994. Low elevation sites (San Luis Valley; 2nd supplemental survey) are a composite of spittlebugs surveyed 26 May and 3 June in sites 1 and 2. Site 3 was excluded because of the presence of *P. simulans*.

generations in Costa Rica (Picado 1970). For the genus *Aeneolamia* in Mexico, *A. occidentalis* completes 1–2 generations per year (Martin et al. 1995), whereas *A. albofasciata* is capable of 2–3 (Oomen 1975). Unlike most grassland cercopids, eggs of *A. flavilatera* apparently do not enter into diapause (Fewkes 1969, Wiedijk 1982); this allows the species to achieve 4–6 generations a year in sugar cane fields of Guyana and Surinam (Wiedijk 1982).

Prosapia nr bicincta nymphs peaked in abundance in June, 4–7 wk after the return of the wet season rains. Adults peaked in late June and July. Adult appearance, however, is a poor indicator of local population development because early season peaks represent colonists arriving from other sites where nymphs complete development earlier in the season. In 1992, for instance, colonist arrival was synchronous in all 3 paddocks; because of differences in nymph development, however, arrival coincided with teneral appearance in C2 and S1, but occurred in advance of teneral appearance in S2. Adult population size, however, might be predicted from early season nymph abundance because seasonal adult abundance varies between paddocks and years in the same way nymph abundance does.

Surveys revealed that spittlebug phenology varied substantially on both a local and regional scale. Within 10 km of Monteverde, survey paddocks there were resident *P. nr bicincta* populations 2.5 wk more advanced. Locally, however, there was no evidence that variation in population initiation dates and development time depended on paddock, year, or dominant forage.

Assessing Evidence for Froghopper Movement. These detailed population surveys offer new information about froghopper dispersal. Two classic forms of evidence for long distance dispersal have been elaborated from studies of froghopper relatives, the leafhoppers (Cicadellidae). The 1st is the arrival of alates to an area before the maturation of local populations (Drake and Chapman 1965). The current population studies in Monteverde have shown that adult *P. nr bicincta* can arrive in local pastures before a real contribution from local nymphs. Early appearing froghoppers are not overwintering adults because *P. nr bicincta* survives the dry season (November–April) only as diapausing eggs (Peck 1996).

The 2nd is the arrival of adults to a region where the population cannot persist all year (Poos 1932, DeLong and Caldwell 1935, Medler 1957, Wallis 1962). Because female and nymphal *P. simulans* were absent in survey paddocks, adult males must be considered immigrants, either unsuccessful colonists or migrants in transit. Populations of this species do not complete their life cycle locally. The abrupt peaks, particularly in 1991–1993, indicate a rapid and synchronous arrival as well as an abrupt departure. Although adult longevity is unknown for this species, adult congeners live up to 7 wk (Peck 1998a); thus, it is unlikely that males die rapidly enough to cause the sharp declines in density. Population curves therefore indicate that male immigrants arrive synchronously and may just be transients in passing. These conclusions are corroborated by sticky trap results that show a relatively high flight activity for *P. simulans* in Monteverde (Peck 1996).

Evidence for immigration is further supported by the abrupt (Drake and Chapman 1965, Carlson et al. 1992) and synchronous (Medler 1957) appearance of alates. Although peak abundance of nymphal instars varied substantially from one paddock to the next, early season adult male *P. nr bicincta* peaks are distinct, synchronous across paddocks, and occur on dates clearly disassociated from the previous life stage. *P. simulans* males appeared abruptly in every paddock-year, and peaked on the same dates between all 3 paddocks within each year. The synchronous arrival and uniform settling indicate an arrival en masse. These colonization events may also explain why nymphal abundance varied twice as much as adults among paddock-years: site differences in the population density of resident spittlebug populations is obscured in the adult stage because of movement.

Local appetitive movement has been consistently recognized as a factor influencing local population fluctuations in the superfamily Cercopoidea (Matsumoto et al. 1988, Nilakhe and Buainain 1988). This local movement is best documented as the exploita-

tion of nearby food plants and crops not used by nymphs (Nilakhe 1985, Peck 1998b) or movement between fields in response to habitat alterations (Weaver and King 1954, Wiegert 1964, Wiedijk 1982). I know of no study that has yet documented migratory movement or long-distance dispersal among cercopids but the current evidence suggests that this is not outside the realm of possibility.

It was not possible to absolutely determine the source populations of colonists. It is certain, however, that adult *P. nr bicincta* could invade Monteverde pastures from areas within 10 km where environmental conditions promote earlier development of spittlebug populations. After they mature, adults become available as migrants. The climate of the potential source region is reported to have an abbreviated and more humid dry season so there may be continual presence of the insect or earlier rains may lead to earlier population initiation.

Prosapia simulans immigrants in Monteverde are probably altitudinal migrants. Arrival of froghoppers from San Luis to Monteverde could depend on uphill convective winds originating from the Pacific coast. The breeding population nearest to survey paddocks was 1.9 km distant and 375 m lower in elevation. The intervening habitats were largely precipitous secondary forest and scrub that were not suitable for supporting substantial *P. simulans* populations. Adult migrants of this species were also captured in a more distant pasture 3.4 km from San Luis breeding grounds and 485 m higher in elevation (1,450 m). Adult male *P. simulans* are therefore capable of flights at least 3–4 km.

No long-distance tracking studies on froghoppers have been published. Up to now the longest estimation of flight by this group was determined in wind tunnel studies to be 3.35 km (Nilakhe and Buainain 1988). These estimates from Monteverde and Nilakhe and Buainain are conservative; it would not be surprising to discover that froghoppers are capable of flights much longer given the role of wind patterns in orienting, facilitating, and augmenting the long-distance flights of other homopterans (Pienkowski and Medler 1964, Mikkola 1986, Seino et al. 1987). Because of the large variation in the regional phenology of *Prosapia*, it is unnecessary to invoke very long-distance displacement to explain the Monteverde colonists, certainly not on the continental scale of well-known migrants like the potato leafhopper (Medler 1957, Pienkowski and Medler 1964, Carlson et al. 1992, Taylor and Shields 1995), sixspotted leafhopper (Wallis 1962, Chiykowski and Chapman 1965, Drake and Chapman 1965) or other long-distance homopteran dispersers (Medler 1962).

Results from both field and sticky trap surveys lead to the suggestion that a male bias for dispersal exists in both *P. nr bicincta* and *P. simulans*. Male *P. nr bicincta* show more early season peaks than females, achieve a premature peak abundance more often, and show more synchrony in appearance between paddocks within a single year. Sticky trap collections showed females to be less active fliers than males (Peck 1996).

In the case of *P. simulans*, females rarely make it from breeding grounds to Monteverde and the male immigrants have greater flight activity than froghoppers of local origin (Peck 1996). It is unlikely that female *Prosapia* are flying above and beyond Monteverde because the genus has a brief premating period (2–9 d, Peck 1996) and there is no evidence, at least among the Cercopidae, for reproductive diapause. Gravid *Prosapia* females fly poorly or do not fly at all (unpublished data). Poor flight ability and time spent ovipositing may cause a "lack of opportunity" among females that reflects both a narrow window of flight opportunity and capability (Peck 1998b). This case of a male-biased propensity for dispersal merits further examination. The oogenesis-flight syndrome, which implicates postteneral and prereproductive adults in most migratory events (Johnson 1969, Rankin et al. 1986), is the only major generalization that attempts to link gender and flight behavior. There is no evidence at hand, however, to offer insight into the apparent problem of male froghoppers emerging before females and leaving the habitat. Two untested possibilities are that this behavior is linked to degradation of habitat to which only males can physically respond, or it is non-adaptive behavior linked to the aboriginal habitat. The association between *P. nr bicincta* and *P. simulans* and pastures could be considered relatively new, initiated with the substitution of forests by pastures dominated by African grasses.

The detection of protandry and male-biased dispersal in *P. nr bicincta* adults in local paddocks depended on long-term and detailed population surveys. Factoring out such phenological phenomena is more difficult in short-term studies that fail to identify year-to-year variation and in less detailed studies that do not distinguish among all life stages. An intimate view of the progression from one life stage to the next offers the best resolution of local phenology for exposing immigration from the background fluctuations of resident populations. Determining that *P. simulans* did not complete its life cycle in the zone (and that all adults are immigrants) largely depended on noting teneral adults, especially because *P. simulans* males are frequently seen copulating with *P. nr bicincta* females in the field (unpublished data) and could thereby be mistaken for color morphs or successful breeders. There is no evidence to suggest that these 2 species successfully hybridize (Peck 1996).

Implications for Management. Even the most detailed among other studies of grassland cercopids has failed to provide data on the density of all nymphal and adult life stages and thereby fully link the population dynamics of nymphs with adults (Peck 1996). Some studies, for instance, have drawn interpretations from sweep net and light-trap surveys that may not be indicative of the actual phenology of local populations (Beck 1963, Fagan and Kuitert 1969, Beck and Skinner 1972, Enkerlin and Rosell 1979). Others have failed to assess or distinguish among all 5 nymphal instars (Byers 1965, Washbon 1968, Picado 1970), and only 1 study of nymphs has reported data on the occurrence of teneral adults remaining in spittle masses (Washbon

1968), the earliest indication of maturing nymph populations. Such studies offer an incomplete, if not imprecise, picture of population dynamics. For instance, sampling programs that ignore nymphs yield peaks that do not necessarily correlate with nymph generations and thereby could misinterpret the number of generations and lose the resolution to predict the phenology of local populations.

Unlike other regions with pest cercopids, pasture managers in Monteverde must contend with a single generation a year. Because nymphs require 34–98 d to mature (Peck 1998a), there is a relatively wide window of opportunity to apply pest control measures aimed at suppressing spittlebug populations before they advance to economically important levels.

Aside from number of broods, the impact of cercopids on forage production, quality, and persistence will depend on the synchrony and magnitude of attack, especially for a tolerant forage like East African star grass. With as many as 277 nymphs per square meter, pastures may suffer extreme water stress during periods of peak abundance, just when farmers depend on a wet season flush of grass. Economic thresholds have not yet been determined for cercopids on any forage species. Two studies, however, suggest values for determining the severity of infestation. Padilla and Esquiliano (1966) designate "severe" infestations as >30 nymphs per square meter and >25 adults per 50 sweeps, above which application of pesticides is recommended. Enkerlin and Morales (1979) report levels modified from Velasco and Sifuentes (1970) where "high" infestations are >46 nymphs per square meter and 150 adults per 50 sweeps, and "severe" infestations are above 60 nymphs per square meter and 250 adults per 50 sweeps. In Monteverde, *P. nr bicincta* nymphs achieved 30 nymphs per square meter in 9 of 12 paddock-years, and 60 in 8 paddock-years (based on 4 quadrats in 1991 and 8 in 1992–1994). *P. nr bicincta* adults surpassed 25 per 50 sweeps in 11 of 12 paddock-years and 250 in 1 paddock-year (based on 4 by 50 sweeps). In the face of so much variation in the designation of infestation severity, the establishment of economic thresholds must take into account forage species, pest species, and their shared habitat.

Management of pest cercopids will be challenged by both the profound variation in phenology over a small geographic area and the vagility of adults. Within and between farms situated in the Monteverde "milkshed," (the area from which milk is supplied to the local dairy plant) the nature of the impact of pest cercopids may vary extraordinarily given variation in species composition and the timing of outbreaks. Understanding the dispersal capabilities of insects—particularly the timing of migration, immigration and emigration rates, colonist reproductive capacity, and pattern of population redistribution—is critical for implementing effective pest control strategies (Joyce 1981, Stinner et al. 1983). Clearly, management of grassland cercopids must be considered on a regional scale because events that occur elsewhere can influence local population dynamics and jeopardize the effectiveness of control techniques that are applied

locally. Colonization also complicates the prediction of pest status and forces managers to confront the mechanisms of froghopper damage to host plants, thereby anticipating the potential impact that adult immigrants have on pastures suffering damage from high population densities of resident nymphs. Finally, this study exposes the risk of misinterpretations caused by scouting programs that rely only on sweep net surveys, and underline the value of distinguishing among all life stages to gain a detailed picture of the sequence and timing of life history events.

Acknowledgments

I am indebted to Joe and Jean Stuckey for generous access to their farm for pasture surveys and their support in many other aspects of this research. I thank Jacqueline Madrigal for her dedicated field assistance in 1992 and 1993, John Campbell for precipitation data, Jorge Ruiz Ch. of the Monteverde Producer's Association, and other friends and the many people of Monteverde, especially Stella Wallace. Danis Brenes, Rafa Leitón, and Fabio Cambonero Brenes provided access to their San Luis farms for supplemental surveys. I thank Richard Root, Maurice Tauber, Alison Power of Cornell University, and 2 anonymous reviewers for comments on early versions of the manuscript. This work was supported by grants from the Cornell Graduate School, the Organization for Tropical Studies, the Cornell International Institute for Food, Agriculture and Development, the Mario Einaudi Center for International Studies at Cornell, the Andrew W. Mellon Foundation, and Sigma Xi.

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Received for publication 11 April 1997; accepted 9 February 1999.

Reflex Bleeding in Froghoppers (Homoptera: Cercopidae): Variation in Behavior and Taxonomic Distribution

DANIEL C. PECK¹

Department of Entomology and Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853-2701

Ann. Entomol. Soc. Am. 93(5): 1186-1194 (2000)

ABSTRACT Reflex bleeding in New World froghoppers is described in detail for the first time. *Prosapia* sp. n. adults exude hemolymph from rupture lines in pretarsal pads when attacked by predators. After an assault, food access permitted replenishment of exudate volume within 6 h. A survey of New World Cercopoidea (53 species) demonstrated the behavior to be synapomorphic in the predominantly aposematic family Cercopidae, but not present in the largely cryptic Aphrophoridae and Clastopteridae. A comparative study of four species [*Iphirrhina quota* (Distant), *Mahanarva costaricensis* (Distant), *P. plagiata* (Distant), and *Prosapia* sp. n.] showed that total volume of exudate, volume per weight, and response to general versus localized assaults varied among sexes, species, and habitats. Laboratory and field bioassays failed to demonstrate mechanical or chemical deterrence. In tandem with warning odors, however, conspicuousness coloration and reflexive discharge of blood form an elaborate warning signal in cercopid froghoppers, probably functioning as a startle stimulus that permits escape by jumping.

KEY WORDS *Iphirrhina quota*, *Mahanarva costaricensis*, *Prosapia plagiata*, aposematism, insect defense, warning coloration

REFLEX BLEEDING is the defensive discharge of blood (Cuenot 1896). Certain insects have the ability to autohemorrhage, or bleed spontaneously, when assaulted (Hollande 1911), thereby exposing attackers to deterrent factors in the hemolymph. Blood—no matter how dispensed—can have multiple defensive roles: it may function as a physical deterrent, as a chemical deterrent when fortified with distasteful or odoriferous chemical factors, and even as a constituent of exocrine gland secretions (Blum 1981).

Among insects that bleed reflexively, blood is most commonly implicated as a mechanical deterrent (Happ and Eisner 1961, Wallace and Blum 1971, Benfield 1974, Blum and Sannasi 1974). Hemolymph that is sticky, viscous, and rapidly coagulating poses an effective defense against arthropod predators such as ants, which cease their attack to groom. Other reflex bleeders have been shown to repel enemies by virtue of chemical components in the blood that are distasteful or noxious (e.g., Blum and Sannasi 1974, Carrel and Eisner 1974, Moore and Brown 1981, Eisner et al. 1986).

In the course of other studies it was discovered that froghoppers of the New World genus *Prosapia* (Cercopidae) emit a fluid from pretarsi when disturbed. Until now, only camouflage coloration, jumping ability (Hamilton 1982), and escape warning coloration (Thompson 1973) have been considered in the defense repertoire of froghoppers in the superfamily

Cercopoidea. Moreover, reflex bleeding has not been studied in detail among the Homoptera although it has been reported as a defensive mechanism in some Pseudococcidae, Cicadellidae, and Cercopidae (Hollande 1911). *Prosapia* and its relatives are widely distributed pests of forage grasses and sugar cane (Fewkes 1969, Peck 1998), which compels us to study a behavior that influences the impact of their natural enemies. For these reasons, the ability of cercopids to autohemorrhage merits a detailed examination.

Prosapia and its confamilials are largely bright-colored and conspicuous. Reflex bleeding, like other insect defenses, is frequently correlated with conspicuousness (Boros et al. 1991), suggesting that *Prosapia* is aposematic. If it serves as a defense, reflex bleeding in combination with ability to escape may render the insect sufficiently "unprofitable" (sensu Baker and Parker 1979) for enemies so as to promote the evolution of warning signals.

Here I examine several aspects of reflex bleeding behavior among certain neotropical froghoppers including exudate capacity and replenishment, sex differences, and interspecific variation. This report also describes the response of froghoppers to varying conditions of attack and recovery, the distribution of the character within the superfamily Cercopoidea, the variation in behavior among four species from two different habitats, and the role of reflex bleeding in deterring natural enemies. Finally, the relationship between reflex bleeding and the evolution of warning signals is considered.

¹ Current address: International Center for Tropical Agriculture (CIAT), A.A. 6713, Cali, Colombia.

Materials and Methods

Description of Site and Fauna. Most of these studies were carried out from 1991 to 1994 in Monteverde, Costa Rica, a seasonally wet region in the Tilarán Mountains. The landscape is a mixture of pastures and tropical premontane and lower montane cloud forest, 1,300–1,600 m elevation. This area supports a high diversity of Cercopoidea froghoppers, including representatives of all three New World families, the Cercopidae (24 species), the Clastopteridae (three species) and the Aphrophoridae (three species) (Peck 2000).

Reflex bleeding in four species of froghoppers (Cercopidae: Tomaspidae) was studied in detail. All four are conspicuous diurnal feeders on the xylem sap of their host plants. Two grassland species are abundant in roadsides and pastures during the rainy season. An undescribed species of *Prosapia* (hereafter called *Prosapia* sp. n.) is the principle forage pest and most common froghopper in the region, displaying a high contrast color pattern with a crimson venter and a black dorsum marked by three transverse red stripes. *P. plagiata* (Distant) is a minor pasture pest with a dark brown venter and lighter brown dorsum; $\approx 8\%$ are red morphs. The other two test species occur on hosts in roadsides and forest gaps. *Iphirrhina quota* (Distant) feeds on plants of the Piperaceae and has a red venter and dorsum. *Mahanarva costaricensis* (Distant) variety *semimaculata* (sensu Thompson 1997) feeds on *Heliconia tortuosa* Griggs and adults display a high contrast pattern of black, metallic blue, and orange. The approximate length of adults is 7.5, 10.0, 13.3, and 19.2 mm for *P. plagiata*, *Prosapia* sp. n., *I. quota*, and *M. costaricensis*, respectively.

Bleeding Behavior in *Prosapia* sp. n. To aid studies of reflex bleeding in adult *Prosapia* sp. n. S-shaped wire handles (≈ 2 mm tall) were attached to the pronota with rapid-bonding glue. After recovering in cages with food for at least 48 h, individuals could be picked up by their handles without inducing bleeding and tethered with polyethylene tubing. Tethered individuals were used as follows: (1) to observe bleeding under the dissecting scope; (2) examine the response to mechanical stimuli that simulated predator attacks, including pinching with forceps and touching with a hot needle; and (3) to report the outcome of staged encounters with potential enemies. The cellular components of fluid from the pretarsi and hemolymph from a cut antenna were examined with Sarkaria-Bettini-Patton (SBP) stain immediately after being collected in capillary tubes.

Recovery Experiment. Preliminary tests in 1993 indicated that once defensive reserves were spent, froghoppers did not recover their ability to bleed without access to food. Therefore, the ability of male and female *Prosapia* sp. n. froghoppers to recover their capacity to bleed was tested under four treatment combinations comprising individuals initially assaulted or not assaulted and subsequently allowed to recuperate with or without access to food.

Before treatment, all individuals fed undisturbed on host plants for at least 48 h. Froghoppers in the assaulted treatment were held by hand and induced to bleed by pinching and prodding the legs and venter with needle-nosed forceps for 1.5 min. Injuring the insects was avoided to ensure that no hemolymph was lost from wounds. Fluid emission was calculated by drawing the pretarsal exudate from all six legs up a glass microcapillary tube (0.4 mm diameter) and measuring the height to the nearest 0.5 mm.

Ten males and 10 females were arbitrarily assigned to each of the four treatments. Each of the 10 replicates comprised a pair of pots under individual sleeve cages: empty (no food) or with a local host (with food), East African star grass (*Cynodon nlemfuensis* Vanderyst). Each pot housed two males and two females. Individuals not assaulted were put directly in sleeve cages, whereas assaulted individuals first received a dot of blue enamel paint. After remaining undisturbed for 6 h under ambient conditions, each froghopper was removed and assaulted (1.5 min) to determine posttreatment exudate volume. Data were analyzed with split-plot analysis of variance (ANOVA) where paired empty and planted pots were considered random block effects.

Taxonomic Distribution. To determine the distribution of reflex bleeding among related taxa, 53 froghopper species from Costa Rica and elsewhere in the New World were tested for this character. Signs of bleeding were recorded after a new species or sex was captured in the field. This was followed as needed by pinching the legs and venter with forceps, and lastly, by tasting the venter and legs for the distinctive-tasting fluid.

Comparative Behavior. Differences in how froghoppers autohemorrhage were tested by comparing the behavior among four species from two habitats. In their pasture habitat, *Prosapia* sp. n. and *P. plagiata* may be more likely to encounter abundant ground-dwelling arthropod predators, whereas *I. quota* and *M. costaricensis*, normally feeding at sites 1–4 m above the ground in roadside/forest gap habitats, might encounter more avian predators. Initial evidence gathered in 1993 also suggested that *Prosapia* was most responsive to localized attacks (such as pinching with forceps), whereas *I. quota* and *M. costaricensis* bled most vigorously in response to broadly generalized attacks (such as hand removal from the host plant). These species were therefore tested in 1994 for differences in their reaction to varying artificial assaults.

Test froghoppers were removed from their feeding sites in the field or in the greenhouse by seizing them from the back with three fingers (at the head and each side of abdomen). They were then assaulted (as in the recovery experiment) for 2 min, placed in a vial without food for 15 min, and assaulted again for an additional 30 s (or until they stopped bleeding). The volume of pretarsal exudate was collected and measured at three stages: (1) after the initial seizing attack, (2) after the first pinching attack, and (3) after the second pinching attack. Each individual was preserved in 70% ethanol until oven-dried and weighed to the nearest

0.01 mg. Ten froghoppers of each sex were tested, except male *M. costaricensis*, which were unavailable at the time of the experiment.

The effect of species, sex, and dry weight on total volume of exudate (square-root transformed) was tested with analysis of covariance (ANCOVA). ANOVA was used to test the effect of species and sex on the proportion of total volume exuded (square-root transformed) in response to the seizing attack. Kruskal-Wallis and Wilcoxon rank-sum nonparametric tests were used to test the effect of species and sex, respectively, on the proportion of remaining fluid exuded in response to the first pinching attack.

Encounters with Predators. A series of bioassays was performed with *Prosapia* sp. n. froghoppers and sympatric predators to test the ability of enemies to elicit reflex bleeding and whether this response deters attacks. Encounters between froghoppers and ants (*Odontomachus opaciventris* Forel), fire ants [*Solenopsis geminata* (F.)], and rove beetles (*Psephenus* sp.) were staged in the laboratory. Predators were held with forceps and encouraged to bite tethered adults. In other tests, enemies were allowed to initiate their own attacks while enclosed with froghoppers in petri dish arenas (5 and 9 cm diameter) lined with white filter paper to reveal production of exudate; 1–2 froghoppers were confined for up to 1.5 h with two *O. opaciventris* (four trials), 10–20 fire ants (four trials), or two to four rove beetles (three trials). Finally, encounters in the field were staged between tethered froghoppers and fire ants, *O. opaciventris*, [*Eciton burchellii* (Westwood)], funnel spiders (Agelenidae sp.), domestic chickens, and an anole lizard (*Anolis* sp.). Throughout these encounters, reactions from the predators to the froghopper exudate that might indicate mechanical deterrence (such as rapid coagulation and entangling properties) and chemical deterrence (such as distastefulness and repellency) were recorded.

Voucher specimens of the insects examined in these studies were deposited at the Cornell University Insect Collection under Lot #1227.

Results

Bleeding Behavior in *Prosapia* sp. n. When *Prosapia* sp. n. adults were disturbed they exuded droplets of fluid from all six pretarsi. The tarsal pads bulged and ruptured along predetermined lines, apparently in response to hydrostatic pressure generated by contraction of the abdomen (Fig. 1). The fluid was conspicuously yellow to orange to amber in color with a distinct, though not repulsive (to me) taste and odor. Teneral adults could bleed within a few hours after molting from the ultimate instar. The nymphs (spittlebugs) were incapable of reflex bleeding.

The fluid was not sprayed or forcibly discharged. It had a high surface tension, clung to the pretarsus as a cohesive sphere and remained as a globule when transferred accidentally from one leg to another by the insect. With repeated assaults and removal of exudate, a particular leg could produce multiple drop-

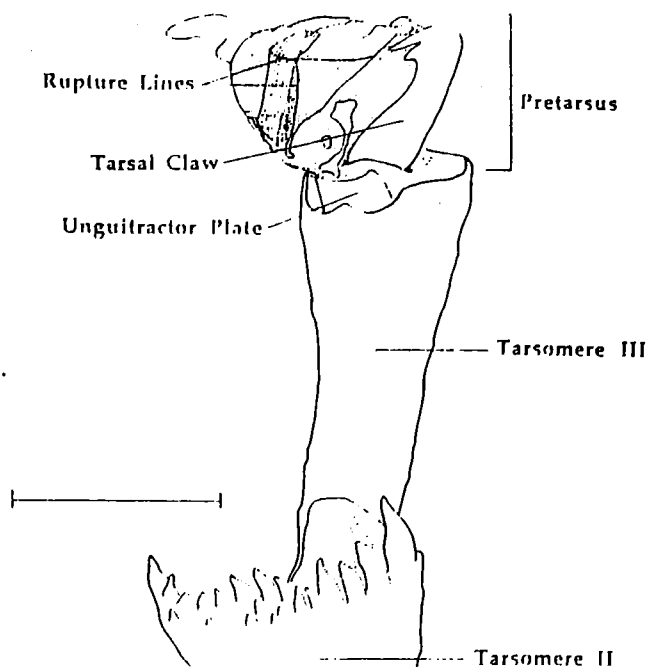


Fig. 1. Mesothoracic pretarsus of *Mahanarva costaricensis* variety *semimaculata*. Hemolymph exudes from rupture lines in the tarsal pads. Scale bar = 0.5 mm.

lets. One female, for example, bled 1.38 μ l from a single hind leg, many times the estimated volume of the leg itself. Otherwise, localized trauma prompted only a single droplet to form on any one pretarsus (Fig. 2).

A variety of evidence demonstrated that the fluid discharge was hemolymph and not the product of an exocrine gland. When manipulations inadvertently injured individuals, they exuded hemolymph from wounds that had a similar viscosity, color, and taste to pretarsal exudate. Staining also revealed the presence of blood plasmatocytes in antennal hemolymph as well as pretarsal exudate.

Froghoppers could autohemorrhage at all six pretarsi simultaneously when seized from their feeding sites (Fig. 2). The response could also be localized to a single leg. I confirmed this by touching the venter of tethered froghoppers with a hot probe. Of 22 touches that elicited bleeding in five adults, 82% caused bleeding from the pretarsus of the leg nearest the probe (with 55% from the nearest leg only); and 95% caused bleeding from the side of the body (left or right) nearest the probe (with 77% from the nearest side only).

Recovery Experiment. Starvation influenced bleeding capability and recovery of froghoppers. ANOVA indicated a significant effect of assault ($F = 10.03$; $df = 1, 57$; $P < 0.005$) and food access ($F = 28.17$; $df = 1, 9$; $P < 0.005$) on exudate recovered after 6 h under experimental conditions; males and females responded similarly ($F = 0.11$; $df = 1, 57$; $P > 0.5$). For individuals not initially assaulted, exudate production fell by half after 6 h without food ($1.05 \pm 0.14 \mu$ l, mean $\pm$ SE) compared with with food ($2.01 \pm 0.28 \mu$ l). Assaulted froghoppers with access to food regained full capacity to bleed ($1.47 \pm 0.25 \mu$ l) within that same



Fig. 2. *Prosapia* sp. n. Simultaneous bleeding from all pretarsi in response to a general assault. Photograph courtesy of Thomas Eisner (September 1986, Archbold Biological Station, Lake Placid, FL).

period. Without food, however, assaulted individuals mustered only a minimal defense ($0.30 \pm 0.08 \mu\text{l}$), although significantly different from 0 ($P = 0.001$) (Fig. 3). Initial volume produced did not differ between assaulted frog hoppers destined for food ($1.76 \pm 0.84 \mu\text{l}$) and no food ($1.79 \pm 0.24 \mu\text{l}$) treatments (t -test, $P = 0.911$), whereas initial volume in assaulted treatments did not differ from final volume for not assaulted/food individuals (t -test, $P = 0.424$).

Taxonomic Distribution. Of the 53 frog hopper species surveyed, 42 exhibited reflex bleeding and 11 did not (Table 1). The nonbleeders were limited to the families Aphrophoridae and Clastopteridae; these families largely comprise inconspicuously-colored insects that display camouflage or disruptive coloration (Peck 1996).

All bleeders were limited to the family Cercopidae and belonged to the tribes Tomaspidini and Ischnorhinini (sensu Metcalf 1961). In contrast to the two nonbleeding families, most Cercopidae exhibit the bright and high contrast color patterns associated with conspicuous insects of the aposematic syndrome (Peck 1996). For example, of the bleeders listed in Table 1, 85% include yellow, orange, and red among

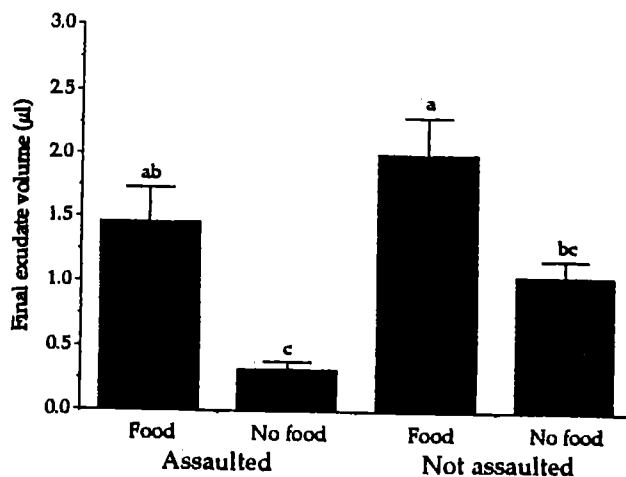


Fig. 3. Volume of exudate recovered from frog hoppers initially assaulted and not assaulted while recovering for 6 h with or without access to food. Bars represent standard errors and columns with different letters are significantly different at $P < 0.05$ (Tukey multiple comparison).

their primary colors, and 55% display those colors in contrasting patterns against a background of black or dark blue. Bright colors and high contrast patterns such as these are thought to be particularly conspicuous to predators having color vision (Guilford 1990b, Schuler and Roper 1992).

Comparative Behavior. For each of the four species examined in detail, emission sites consisted of ruptures in the pretarsal pads and the fluid shared the same distinct color, taste, and odor. In addition, each species exhibited localized bleeding in response to localized assaults and was capable of bleeding from lesions.

Both volume and volume per weight varied among the four test species, volume from 0.75 (*P. plagiata*) to $3.36 \mu\text{l}$ (*M. costaricensis*) and volume per weight from 59.0 (*M. costaricensis*) to $404.9 \mu\text{l/g}$ (*Prosapia* sp. n.) (Fig. 4). ANCOVA (excluding *M. costaricensis*) showed a significant effect of species, but no effect of sex, dry weight, or their interaction (Table 2). Within species, however, sex differences were apparent for *P. plagiata* where males gave more volume per weight ($213.7 \pm 33.9 \mu\text{l/g}$) than females ($126.3 \pm 17.5 \mu\text{l/g}$) (t -test, $P = 0.031$), whereas *I. quota* females gave more total volume and more volume per weight ($3.38 \pm 0.61 \mu\text{l}$, $317.5 \pm 45.9 \mu\text{l/g}$) than males ($1.86 \pm 0.17 \mu\text{l}$, $201.1 \pm 22.7 \mu\text{l/g}$) (t -test, $P = 0.022$, 0.034).

There were also behavioral differences in how defensive reserves were allocated in relation to stage of attack. For the proportion of total volume exuded in response to the initial seizing attack, there was a significant effect of species ($F = 9.116$; $df = 2, 54$; $P = 0.0004$) but no effect of sex ($F = 16.088$; $df = 1, 54$; $P = 0.187$), or species $\times$ sex ($F = 0.045$; $df = 2, 54$; $P = 0.956$). *M. costaricensis* and *I. quota* produced a significantly greater proportion of total exudate in response to the initial seizing attack (mean 0.66 , 0.47 , respectively) than did *Prosapia* sp. n. and *P. plagiata* (mean 0.20 , 0.15 , respectively) (Fig. 5). Of the fluid exuded only in response to the pinching attacks, all species ($P = 0.183$) and each sex ($P = 0.916$) gave a similar

Table 1. Distribution of reflex bleeding among New World Cereopoidae

Family/Tribe/Species	Region	Ability to bleed ^a	Notes
Aphrophoridae			
<i>Aphrophora alni</i> (Fallén)	New York	No	8 males, 2 females tested
<i>Cephus siccifolius</i> Walker	Monteverde, Colombia	No	19 males, 7 females tested
<i>Lepyronia coleoptrata</i> L.	New York	No	1 male, 10 females tested
<i>Lepyronia quadrangularis</i> Say	New Hampshire ^b	No	2 males, 3 females tested
<i>Neophilarnus lineatus</i> L.	New Hampshire ^b	No	4 males, 3 females tested
<i>Philacus spumarius</i> L.	Minnesota, New York	No	33 males, 45 females tested
Clastopteridae			
<i>Clastoptera proteus</i> Fitch	Minnesota	No	1 female tested
<i>Clastoptera (larnata?)</i> Fowler	Costa Rica ^b	No	
<i>Clastoptera</i> sp. 1	Monteverde	No	various tested
<i>Clastoptera</i> sp. 2	Monteverde	No	3 tested (1 male, 1 female)
<i>Clastoptera</i> sp. 3	Colombia	No	10 adults tested
Cercopidae: Tomaspidinae			
Ischnorhini			
<i>Tiodus</i> sp.	Monteverde	Yes	
Tomaspidini			
<i>Aeneolamia albifasciata</i> (Lallemand)	Costa Rica	Yes	
<i>Aeneolamia lepidior</i> (Fowler)	Costa Rica, Colombia	Yes	
<i>Aeneolamia postica</i> (Walker)	Monteverde	Yes	
<i>Aeneolamia reducta</i> (Lallemand)	Costa Rica ^b , Colombia	Yes	
<i>Aeneolamia varia</i> (F.)	Colombia	Yes	
<i>Deots flavopicta</i> (Stål)	Brazil	Yes	
<i>Huaina inca</i> (Guérin-Méneville)	Monteverde	Yes	
<i>Iphirrhina quota</i> (Distant)	Monteverde	Yes	
<i>Iphirrhina</i> sp. 1	Monteverde	Yes	
<i>Iphirrhina</i> sp. 2	Nicaragua ^b	Yes	
<i>Isozulia astralis</i> (Distant)	Ecuador	Yes	
<i>Kanaima vittata</i> (Walker)	Brazil	Yes	
<i>Mahanarva andigena</i> (Jacobi)	Colombia, Ecuador	Yes	
<i>Mahanarva costaricensis</i> (Distant)	Monteverde	Yes	
<i>Mahanarva insignita</i> (Fowler)	Costa Rica ^b	Yes	
<i>Mahanarva phantastica</i> (Bredt)	Colombia	Yes	
<i>Mahanarva</i> sp. n.	Colombia	Yes	
<i>Maxantonia mylabroides</i> (Fowler)	Monteverde	Yes	
<i>Notozulia rubrivittata</i> (Berg)	Brazil	Yes	
<i>Ocoaxo (inflexa?)</i> (Nast)	Monteverde	Yes	
<i>Ocoaxo (septemnotata?)</i> (Distant)	Monteverde	Yes	
<i>Ocoaxo</i> sp. 1	Monteverde	Yes	
<i>Prosapia bicincta</i> (Say)	Florida	Yes	
<i>Prosapia ignipictus</i> (Fitch)	New Hampshire ^b	Yes	
<i>Prosapia plagiata</i> (Distant)	Monteverde	Yes	
<i>Prosapia simulans</i> (Walker)	Monteverde, Colombia	Yes	
<i>Prosapia</i> sp. n.	Monteverde	Yes	
<i>Sphenorhina conspurcator</i> (Distant)	Monteverde	Yes	
<i>Sphenorhina distinguenda</i> (Walker)	Costa Rica	Yes	
<i>Sphenorhina</i> sp. 1	Colombia	Yes	
<i>Sphenorhina</i> sp. 2	Ecuador	Yes	
<i>Tomaspis biolleyi</i> (Distant)	Monteverde	Yes	
<i>Tomaspis</i> sp. 1	Monteverde	Yes	
<i>Zulia carbonaria</i> (Lallemand)	Colombia	Yes	
<i>Zulia pubescens</i> (F.)	Colombia, Ecuador	Yes	
<i>Zulia villor</i> (Fowler)	Costa Rica	Yes	
<i>Zulia</i> sp. n.	Colombia	Yes	
Undet. sp. 1	Monteverde	Yes	
Undet. sp. 2	Monteverde	Yes	
Undetermined			
Undetermined sp. 1	Monteverde	Yes	
Undetermined sp. 2	Monteverde	Yes	

^a All bleeding species include both males and females.^b Personal communication V. Thompson (Roosevelt University, Chicago, IL).

proportion to the first pinching (mean 0.75, 0.71, 0.77, 0.78 for *M. costaricensis*, *I. quota*, *Prosapia* sp., and *P. plagiata*, respectively; mean 0.77, 0.75 for males and females, respectively).

An additional difference between the species was shown in response to the initial seizing attack. The *Prosapia* species tended to bleed from one or two legs

at a time, whereas *M. costaricensis* commonly bled from four and *I. quota* from six tarsi simultaneously. For example, of a series of 10 *I. quota* tested in 1993, one did not bleed, nine bled in three legs or more, seven in five legs or more, and six in all six legs. *M. costaricensis* rarely bled from the two front tarsi, which they curiously held in the air while on host plants.

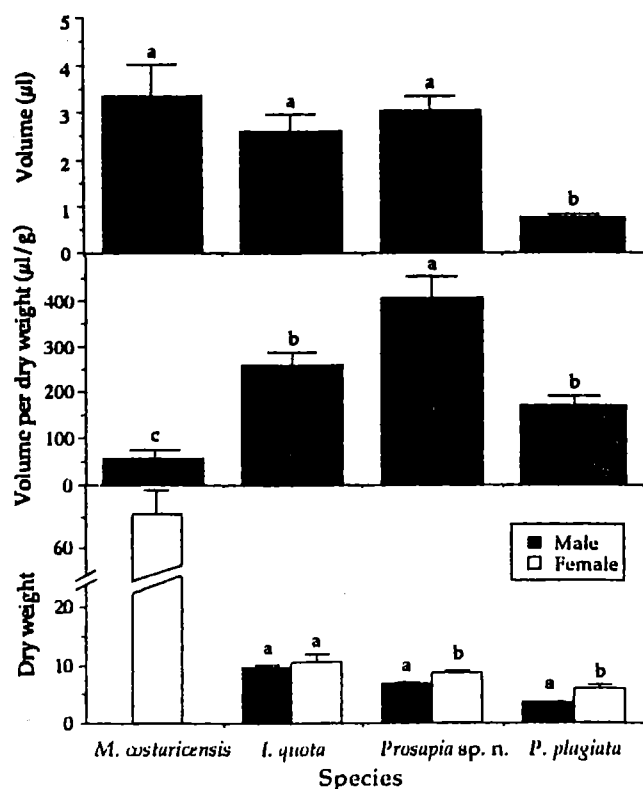


Fig. 4. Dry weight and comparative exudate production (total volume and volume per dry weight) in four frog species. Volume is the sum of exudate collected over the three attack stages. Mean based on $n = 10$ males and females for each species except *M. costaricensis* where $n = 10$ females only. Bars represent standard errors and columns with different letters are significantly different at $P < 0.05$ (Wilcoxon rank-sum nonparametric test for dry weight; Tukey multiple comparison, square-root transformed, for exudate production).

Encounters with Predators. Tethered *Prosapia* sp. n. adults bled reflexively when bitten by rove beetles, *O. opaciventris*, and fire ants. As with the artificial assaults, froghoppers most commonly bled from the pretarsus of the attacked leg and also exuded hemolymph directly from lesions. Only fire ants attacked froghoppers in the petri dish arenas, causing localized bleeding and up to 10 blood stains after a 5-min bout of attack. Other tests demonstrated that arthropod enemies could elicit bleeding in the field. When caught in the webs of funnel spiders, froghoppers bled from pretarsi and wounds before being subdued. Tethered froghoppers forced to encounter trap-jaw ants and fire ants near their nests also bled in response.

There was little evidence for mechanical deterrence. In staged encounters there was only one clear

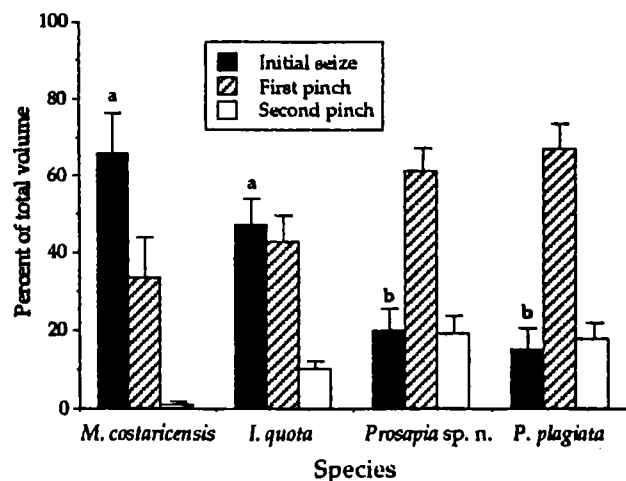


Fig. 5. Proportional allocation of exudate to three stages of attack. Bars represent standard errors. Black columns with different letters are significantly different at $P < 0.05$ (Tukey multiple comparison, square-root transformed).

instance of a predator (fire ant) stopping its attack once the froghopper autohemorrhaged. When rove beetles, *O. opaciventris*, and fire ants came in contact with blood during staged encounters, they were able to quickly and completely wipe the fluid off on the substrate. In general, pretarsal exudate was slow to coagulate and evaporated into a thin film of nonsticky residue.

No clear evidence for chemical deterrence of the exudate was observed. It appeared, however, that froghoppers themselves were distasteful to some enemies. Although *O. opaciventris*, fire ants, funnel spiders, and an anole accepted adult *Prosapia* sp. n. as prey, chickens refused them in one of two trials and *E. burchellii* ants refused them in four of four trials. As an example, in one test I placed a dead cockroach, a freshly decapitated froghopper, and a tethered froghopper at the advancing front of an *E. burchellii* ant column. Although the froghoppers were inspected, only the cockroach was removed by the ants.

Discussion

Reflex Bleeding as a Synapomorphy in the Cercopidae. The defensive use of blood has been reported in representatives of at least 35 families in nine orders: Coleoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, Phasmatodea, and Plecoptera. Although grassland cercopids have long been studied as pests, reflex bleeding has not been described in detail until now. I am aware of only five references to this behavior in the Cercopidae (Hollande 1911, Ulrich 1913, Kershaw 1914, Greathead 1970, Arango and Calderón 1981). It is possible that the ability of other broad taxonomic groups to reflex bleed has been overlooked or, as in the case of scale insects (Hollande 1911, Ferris 1950, McKenzie 1967), not adequately described. The latest summaries of defensive bleeding (Eisner 1970; Blum 1981, Whitman et al. 1990), in fact, have not noted the Homoptera.

Table 2. ANOVA (reduced model) on total exudate volume produced by froghoppers in comparative behavior survey

Source	SS	F ratio	df	Prob > F
Species	3.243	13.518	2	0.0001
Sex	0.332	2.771	1	0.102
Dry weight	0.335	2.794	1	0.101
Species / Sex	0.328	1.366	2	0.264
Sex / Dry wt	0.342	2.849	1	0.097

For the family Cercopidae, reflex bleeding appears to be a shared derived character (synapomorphy). The trait was observed in 42 of the 359 described New World species (Metcalf 1961) and two of the four tribes in the New World clade, subfamily Tomaspidiinae (sensu Fennah 1968). Among the Old World clade, subfamily Cercopinae, *Locris* (Greathead 1970), and *Cercopis* (Hollande 1911) are reported to reflex bleed, and the latter is cited as distasteful (Evans et al. 1985 cited in Evans et al. 1987). Most of the remaining taxa in the family have warning coloration. Therefore, a broader survey will likely show the character to be common to all members of the Cercopidae [1,359 described species world wide (Metcalf 1961)].

Members of the Aphrophoridae and the Clastopteridae apparently cannot reflex bleed. Although only a few individuals ($n = 1-78$) of some species were tested, it is reasonable to conclude that these are reliable negative results given that 94% of the *Prosapia* sp. n. tested in 1994 ($n = 159$) bled in response to assaults. No members of the fourth family of Cercopoidea, the Machaerotidae, have been tested. Given their sister group status to the other Cercopoidea and their lack of warning colors (Maa 1963), the Machaerotidae are probably incapable of bleeding. If this idea holds true, the ability to reflex bleed is a character important to the higher level systematics of the superfamily.

The differences in how froghoppers reflex bleed may represent derived traits with adaptive significance for particular habitats, such as the selective pressure that predators may exert. The particular behavior of *I. quatuor* and *M. costaricensis* to commit most of their defensive resources at once matches predators like birds, which allow only a single opportunity to repel the broadly generalized attack. The particular behavior of *Prosapia* sp. n. and *P. plagiata* to respond to localized attacks and not commit all resources at once matches abundant ground-dwelling invertebrate enemies such as ants.

Statistical analyses show that in addition to the type of stimulus, volume production (defensive capability) depends on size, sex, and species. Volume per dry weight varied nearly sevenfold; and the largest species, *M. costaricensis*, did not produce more volume than *Prosapia* sp. n., a species that is nearly an eighth its mass. Sex-related trends may be obscured by reproductive status because it is reasonable to suggest ovarian development reduces female defensive reserves by displacing hemolymph capacity. Little is known about inter- or intraspecific variation in defensive secretions although a few instances of sex differences in reflex bleeding have been reported [the blister beetle *Lytta* (Sierra et al. 1976) and the stick insect *Diaperomera veliei* Walsh (Sivinski 1980)] and secretory volume has been shown to increase with mass in other chemically defended insects (Whitman et al. 1992). Froghoppers offer an opportunity to study such variation within a clade where the defense apparently evolved in a common ancestor.

Reflex Bleeding and the Evolution of Warning Signals. A dramatic correlation exists between reflex bleeding and conspicuous coloration among froghoppers. The four study species are also relatively inactive diurnal feeders with exposed feeding and mating behavior, traits consistent with an aposematic lifestyle (Bernays and Montllor 1989, McIver and Lattin 1990).

Warning colors and reflex bleeding in the Cercopidae may be accompanied by alerting odors that serve as an additional warning signal. It is known that the aposematic *Cercopis vulnerata* Rossi (Cercopinae) contains methylalkylpyrazines (Moore et al. 1990). Pyrazines are common alerting odors in nature (Rothschild 1964, Rothschild and Moore 1987), thought to function as potent warning signals for vertebrate predators in combination with negative circumstances (Kaye et al. 1989). Pyrazines have been shown to elicit aversion behavior in birds, particularly in combination with aposematic colors (Guilford et al. 1987, Rowe and Guilford 1996). Therefore, in at least some Cercopidae, warning odors are probably also emitted with the blood, an explanation for the similar taste and smell of the reflex bleeding fluid across taxa.

What is the function of conspicuous color, reflex bleeding, and alerting odors in the Cercopidae? Diverse evidence leads to the conclusion that reflex bleeding behavior in froghoppers functions in defense. Because froghoppers hold their legs distal to the body at rest, rupture sites on the pretarsi are apt to first contact an approaching enemy. Bleeding is reflexive, localized, and elicited by predaceous arthropods that share the froghoppers' habitat. Froghoppers that survive attacks can recover their ability to bleed within 6 h provided they have access to food sources.

Despite this suite of characteristics, the defensive function of antihemorrhage in froghoppers is unclear compared with certain other taxa where mechanical and chemical repellency is conclusively implicated. There are clear examples of exuded hemolymph operating to entangle predators (Happ and Eisner 1961, Wallace and Blum 1971, Benfield 1974, Matsuda 1982), to render the insect distasteful or toxic (Carrel and Eisner 1974, Heads and Lawton 1985), or both (Blum and Sannasi 1974, Eisner et al. 1986). It may be that the blood of froghoppers does not dispense deterrents other than warning odors. Alternatively, it may be that the blood is only deterrent if associated with an internal toxin a predator experiences after consumption (Krall et al. 1997).

The unconvincing evidence for traditional mechanical and chemical deterrence leads to the suggestion that reflex bleeding in froghoppers functions in part as a startle stimulus (Sargent 1990), comprising two components: physical discharge of blood and the chemical warning odor. Because froghoppers are skilled jumpers, any deterrent need only cause an attacker to hesitate momentarily for the insect to hop to safety. Reflex bleeders in other insect orders are often much less mobile (Happ and Eisner 1961, Wallace and Blum 1971), and therefore may require entangling substances that serve to terminate an attack. For froghoppers, a startle defense may be broadly effective

against the diversity of invertebrate and vertebrate predators that they encounter. Reflex bleeding in the stonefly *Peltoperla maria* Needham & Smith might have a similar function. Although the hemolymph is an effective mechanical deterrent to ants, Benfield (1974) suggested that "explosive autohemorrhage" may repel initial assaults by mice. Given that entangling substances are largely ineffective against mammals, the 'explosion' may provide *P. maria* flies with an opportunity to escape through flight.

The nature and origin of the precise defensive factors (pyrazines or others) in the Cercopidae remains undetermined. Reflex bleeders in other insect orders are known to be defended by allomones synthesized de novo (Deroe and Pasteels 1977, Moore and Brown 1981), as well as directly sequestered (Boros et al. 1991) or endogenously transformed from host plants (Eisner et al. 1978, Daloze et al. 1981). Among froghoppers, the diverse range of host plants suggests biosynthesis rather than sequestration. Hosts of the four test species in this study, for instance, include 15 genera from eight plant families (Peck 1996). The diverse grassland froghoppers of the Neotropics rely almost exclusively on graminoid hosts and this plant group is not known for defensive secondary compounds.

Jumping ability is hypothesized to be the defense that maintains a form of warning coloration in *Philaenus spumarius* L. (Aphrophoridae) (Thompson 1973). But in the largely tropical Cercopidae, evidence suggests a more cohesive and elaborate defensive package to link the warning signal with the unprofitability. The warning signal probably consists of visual aposematic coloration and behavior, physical/visual startle through reflexive discharge of blood, and probable olfactory warning odors dispensed in the blood. The unprofitability advertised by these signals probably consists of escape ability through jumping and possible defensive deterrents in the blood. For reflex bleeding in froghoppers to constitute a chemical defense per se, however, evidence must be obtained for noxious, or class I, deterrents (Brower 1984). In addition to escape ability, these chemicals could condition color, startle, and odor as aposematic stimuli to naive and experienced predators.

The Cercopidae are consequently among the broadest extant taxa to have a common mechanism for dispensing deterrents. If reflex bleeding in froghoppers evolved only once, then the array of conspicuous color patterns displayed by taxa in this family might be the result of independent subsequent evolution. Froghoppers may therefore serve as model systems to test the role of predators in generating interspecific variation in defensive behavior and to study the circumstances under which individual, kin, and synergistic selection (Guilford 1990a) are responsible for the evolution of aposematism.

Acknowledgments

This manuscript was improved after discussions with Richard Root and the Comparative Ecology Guild (Fritzi Crevstad, Tze-hei Yong, Ruth Hulbauer, Carol Marion, Bernd

Blossey and Ann Herzig), Scott Smedley (Cornell University), and Vinton Thompson (Roosevelt University). Several other people offered thoughtful reviews: Maurice Tauber, Alison Power, Joseph McHugh (Cornell University), and four anonymous reviewers. I thank Matthew Yarrow for assistance in the field, Pamela Ohman for statistical advice, the late William L. Brown, Jr., for ant identification (Cornell University) and William Huber for plant identification (Missouri Botanical Garden). This work was funded in part by the Cornell International Institute for Food, Agriculture and Development, the Organization for Tropical Studies, the Cornell Graduate School, and the Mario Einaudi Center for International Studies at Cornell. This paper is dedicated to the memory of George C. Eickwort.

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DIVERSIDAD Y DISTRIBUCION GEOGRAFICA DEL SALIVAZO (HOMOPTERA: CERCOPIDAE) ASOCIADO CON GRAMINEAS EN COLOMBIA Y ECUADOR

sometido a la:

Revista Colombiana de Entomología

DANIEL C. PECK

Entomólogo/Ecólogo, Proyecto de Gramíneas y Leguminosas Tropicales, Centro Internacional de Agricultura Tropical (CIAT), Apartado Aéreo 6713, Cali, Colombia

Resumen. La diversidad y distribución geográfica del salivazo (Homoptera: Cercopidae) asociado con gramíneas cultivadas y silvestres de Colombia y Ecuador fue analizada con el fin de resumir y difundir nueva información sobre la distribución, hospederos y nomenclatura de las especies económicamente importantes. Registros de distribución de las especies de salivazo fueron obtenidos de recolecciones y observaciones de campo, así como de la revisión de especímenes en cuatro colecciones de diferentes museos. Los datos fueron obtenidos para 21 de los 32 departamentos colombianos y nueve de las 20 provincias ecuatorianas. Se confirmó la presencia de 15 especies en Colombia y ocho en Ecuador para un total de 18 especies de siete géneros: *Aeneolamia*, *Isozulia*, *Mahanarva*, *Notozulia*, *Prosapia*, *Sphenorhina* y *Zulia*. Se encontró un cambio de nomenclatura en *Z. carbonaria*, conocida equivocadamente en Colombia como *Z. colombiana*. Se registraron siete especies por primera vez en Colombia. Dos de ellas son nuevas especies, *Mahanarva* sp. nov. de la Amazonía de Colombia y Ecuador y la Costa ecuatoriana, y *Zulia* sp. nov. de la Costa Pacífica de Colombia y Ecuador. Otra especie, *N. entreriana* en el Dpto. del Meta, representa una posible introducción de Brasil, y la especie *P. simulans* en el Dpto. del Valle del Cauca, representa un posible nuevo invasor de Centroamérica. Para cada especie se resumen los hospederos, distribución a nivel de país, departamento y provincia, y notas taxonómicas. Ya que la composición del complejo salivazo varía sustancialmente entre regiones, se discuten las implicaciones de esta diversidad taxonómica para el manejo de la plaga.

Palabras clave: *Aeneolamia*, caña de azúcar, introducción de especies, *Isozulia*, *Mahanarva*, mión, *Notozulia*, pastos, *Prosapia*, *Sphenorhina*, *Zulia*

LA VARIACIÓN EN la biología, hábitat y taxonomía de las especies de salivazo o mión de los pastos (Homoptera: Cercopidae) compromete seriamente su efectivo manejo por la tendencia a generalizar demasiado en las diversas asociaciones insecto/hospedero/hábitat. En general estos insectos son chupadores del xilema, principalmente de gramíneas neotropicales. Son bien conocidos por la construcción de una masa de espuma protectora durante la fase ninfal, y por la capacidad de brincar y la coloración aposemática típica en los adultos. Sin embargo, existe mucha variación bioecológica, como duración de los estados de vida, sitios de oviposición, y número de generaciones al año. Estos cercópidos son plagas en diversos hábitats porque presentan un amplio rango de distribución geográfico (desde el suroriente de los Estados Unidos hasta el norte de Argentina) y altitudinal (desde el nivel de mar hasta 3000 msnm). Además, estos insectos son plagas tanto en sistemas de pastoreo extensivo como intensivo y atacan casi todos los géneros de pastos económicamente importantes, la caña de azúcar y bajo ciertas circunstancias cultivos como arroz,

césped, maíz y sorgo (Guagliumi 1957, Fewkes 1969a, Souza y Nilakhe 1985, Tashiro 1987).

Son un grupo taxonómicamente diverso; en los neotrópicos, hay muchas especies nativas que atacan gramíneas silvestres o cultivadas, representadas en los siguientes 11 géneros: *Aeneolamia*, *Deois*, *Isozulia*, *Kanaima*, *Mahanarva*, *Maxantonia*, *Notozulia*, *Prosapia*, *Sphenorhina*, *Tunaima* y *Zulia*. Los géneros *Monecphora* y *Tomaspis* originalmente incluyeron especies relevantes pero todas han sido reubicadas en otros géneros. *Delassor* fue descrito en 1948 pero reubicado en *Mahanarva* en 1968 (Fennah 1948, 1968). *Phytozamia* fue creado en 1948 pero sinonimizado con *Sphenorhina* en 1961 (Fennah 1948, Metcalf 1961). Todos estos géneros pertenecen a la subfamilia Tomaspidae (representando los cercópidos del Nuevo Mundo), tribu Tomaspidini (*sensu* Fennah 1968).

A pesar de su importancia económica la taxonomía del grupo no está actualizada. Se presenta un alto grado de variación intraespecífica (Guagliumi 1955, Koller y Valério 1984) y alta convergencia interespecífica en la coloración, lo cual complica la

diferenciación entre especies. Además, pocas de las especies de cercópodos tienen descripciones de la genitalia del macho, una característica clave para la determinación del género y la separación de especies.

Son escasos los estudios y registros publicados sobre el salivazo de los pastos en Colombia y Ecuador. Metcalf (1961) registra la presencia de seis especies distribuidas en Colombia: *Aeneolamia bogotensis* (Distant), *A. lepidior* (Fowler), *A. varia* (Fabricius), *Sphenorhina rubra* (L.), *Zulia birubromaculata* (Lallemand) y *Z. carbonaria* (Lallemand). Desde entonces *A. reducta* (Lallemand) y *Z. pubescens* (Fabricius) (Calderón *et al.* 1982) han sido adicionadas. Para Ecuador, las únicas especies registradas según Metcalf son *Mahanarva andigena* (Jacobi), *M. phantastica* (Breddin), *S. rubra* y *Z. pubescens*. Fennah (1985) adiciona el registro de *Isozulia minor* Fennah.

Por la amplia distribución geográfica y el alto grado de daño al hospedero, el salivazo de los pastos es probablemente el mayor limitante biótico en la producción y sostenibilidad de gramíneas forrajeras mejoradas en los neotrópicos. Por ejemplo, *Brachiaria decumbens* Stapf, un pasto bien conocido por su alta adaptabilidad a los suelos poco fértiles del trópico, es altamente susceptible al salivazo (Keller-Grein *et al.* 1996). Explosión de poblaciones del insecto causa reducción dramática en la producción, calidad y palatabilidad del forraje, reduciendo la persistencia de la pradera y aumentando la degradación ambiental (Valério y Nakano 1987, Valério y Nakano 1988, Hewitt 1989).

Para diseñar un efectivo programa de manejo integrado del salivazo de los pastos, se requiere información precisa sobre la distribución e identificación del complejo plaga. Determinaciones correctas de especies y la elaboración de claves de identificación son de alta prioridad para avanzar en el manejo de la plaga y fomentar nuevas investigaciones (Danks 1988). Se considera que la expresión de resistencia varietal, por ejemplo, depende de la especie de salivazo en particular (CIAT 1999). Por lo tanto es necesario que las tácticas de manejo consideren en detalle la relación salivazo/hábitat/hospedero.

Este estudio se realizó con el fin de preparar un resumen oportuno de la diversidad, clasificación y distribución del salivazo en Colombia y Ecuador. Se necesita esta actualización por la nueva información y resultados que se han sido obtenido de las actividades investigativas realizadas en los últimos cuatro años por el Centro Internacional de Agricultura Tropical (CIAT), la Corporación Colombiana de Investigación Agropecuaria (CORPOICA) y varias universidades en Colombia (Universidad de Sucre, Universidad de la Amazonía,

Universidad de los Llanos, Universidad del Valle, Universidad del Tolima). Este trabajo incluye aclaraciones y cambios en la nomenclatura de las especies del salivazo de los pastos en Colombia y Ecuador, al igual que nuevos registros de distribución.

Materiales y Métodos

La información de distribución fue obtenida de trabajos de campo (1996-2000) y revisión de colecciones en museos (1999-2000). Los datos de distribución fueron recopilados de especímenes mantenidos en museos de cuatro instituciones: el Museo (Británico) de Historia Natural (Londres, Reino Unido) (MBHN), la Universidad de Cornell (Ithaca, Estados Unidos) (UCOR), CIAT (Cali, Colombia) y la Universidad Nacional sede Palmira (Palmira, Colombia) (UNP).

Se confirmó la identificación de cada espécimen adulto. En la mayoría de los casos éste fue apoyado por la comparación y examinación de especímenes tipos ubicados en el MBHN. Ciertas características de la genitalia del macho (edeago, estiletos y láminas genitales) formaron la base para cada determinación, junto con el color y tamaño como características secundarias.

La información recopilada de las colecciones en museos incrementó los registros de distribución y observaciones obtenidas en el transcurso de estudios de campo. En particular se incluyeron estudios realizados en los últimos cuatro años por el CIAT con la colaboración de la UniAmazonia (Florencia), la UniSucre (Sincelejo) y CORPOICA (Reg. 2 C.I. Turipaná, Cereté; Reg. 8 C.I. La Libertad, Villavicencio; Reg. 10 C.I. Macagual, Florencia; Reg. 5 C.I. El Mira, Tumaco) en los departamentos colombianos de Caquetá, Cauca, Córdoba, Meta, Nariño, Sucre y Valle del Cauca.

El análisis de la diversidad y distribución de las especies de Ecuador fue más preliminar con respecto al análisis hecho para Colombia. De las instituciones visitadas, solamente MBHN, UCOR y CIAT tenía datos de distribución disponibles; no se visitaron museos nacionales o regionales en Ecuador. La información del campo fue obtenida en 1998 y 1999 durante una visita (DCP) a Puyo (Prov. Pastaza) coordinada por el Servicio Ecuatoriano de Sanidad Vegetal (SESA) y por especímenes entregados por C. Claus (Programa Forestal Sucumbios, PROFORS), J. Mendoza (Centro de Investigaciones de la Caña de Azúcar del Ecuador, CINCAE) y H. Rogg (Promoción de Exportaciones Agrícolas no Tradicionales, PROEXANT).

Este análisis fue limitado a especies de cercópodos asociadas con gramíneas cultivadas o silvestres. Este subgrupo de especies se determinó por los datos del hospedero encontrados con el espécimen revisado, o en algunos casos por registros en la literatura. Se incluyeron solamente los datos de distribución asociados con los especímenes examinados; los registros de distribución en la literatura no se incluyeron para evitar errores taxonómicos (las pocas excepciones están señaladas). De la misma manera el registro de hospederos fue limitado a datos asociados con los especímenes examinados, con la excepción de los especímenes tipos.

Resultados y Discusión

Material Examinado

De las cuatro instituciones, se examinaron más de 2631 y 85 especímenes montados de Colombia y Ecuador, respectivamente, representando las especies de cercópodos asociadas con gramíneas. En Colombia, se obtuvieron 271, 99, 22 y 20 registros de distribución de CIAT, UNP, UCOR y MBHN, respectivamente, para 21 de los 32 departamentos colombianos. En Ecuador se obtuvieron solamente 5, 0, 5 y 17 registros, respectivamente, para nueve de las 20 provincias ecuatorianas.

Diversidad Genérica

Se encontraron siete géneros de cercópodos asociados con gramíneas en los dos países: *Aeneolamia*, *Isozulia*, *Mahanarva*, *Notozulia*, *Prosapia*, *Sphenorhina* y *Zulia*. El género *Isozulia* no fue registrado en este trabajo asociado con gramíneas para Colombia mientras que *Aeneolamia*, *Notozulia* y *Prosapia* no fueron registrados para Ecuador. Todos estos géneros son conocidos en la literatura por tener especies que son plagas de gramíneas. Sin embargo, fueron los primeros registros de *Notozulia* y *Prosapia* para Colombia y el primer registro del género *Prosapia* en América del Sur. Este género está registrado desde el suroccidente de Canadá hasta Panamá (Hamilton 1977) pero nunca antes en Suramérica (Peck *et al.* en preparación).

Diversidad Específica

Se hallaron un total de 18 especies de cercópodos cuyos hospederos incluyen gramíneas silvestres o cultivadas. De estas, 15 fueron detectadas en Colombia y nueve en Ecuador. El listado en Ecuador incluye *I. minor* (*christenseni*) y *M. phantastica* las cuales fueron descritas originalmente de especímenes colectados en Ecuador

(Metcalf 1961, Fennah 1985) aunque no se examinaron especímenes ecuatorianos en este estudio (Tabla 1). Se encontraron las siguientes seis especies distribuidas en ambos países: *M. andigena*, *M. phantastica*, *Mahanarva* sp. nov., *S. rubra*, *Z. pubescens* y *Zulia* sp. nov.

Se registraron por primera vez en Colombia las siguientes siete especies asociadas con gramíneas: *M. andigena*, *M. phantastica* (Breddin), *Mahanarva* sp. nov., *N. entreriana* (Berg), *P. simulans* (Walker), *Sphenorhina* sp. y *Zulia* sp. nov. En Ecuador los nuevos registros corresponden a las siguientes cuatro especies: *I. astralis* (Distant), *Mahanarva* sp. nov., *Sphenorhina* sp. y *Zulia* sp. nov.

Comparado con otros países neotropicales, Colombia presenta una diversidad relativamente alta de géneros y especies de salivazo. Los únicos géneros no representados en Colombia son *Deois*, *Isozulia*, *Kanaima*, *Maxantonia* y *Tunaima*. Se conoce un registro de *Isozulia* en Colombia pero la única especie registrada, *I. cynanescens* (Lallemand) (*Sphenorhina*), no se conoce en gramíneas (Fennah 1985). En Costa Rica, se han registrado ocho especies y tres géneros del salivazo en gramíneas (Thompson en prensa). En Venezuela se han registrado nueve especies y cinco géneros (Fennah 1949, Guagliumi 1962, DCP registros de MBHN) mientras que en Brasil se han encontrado 16 especies de siete géneros (Guagliumi 1972, Menezes 1982). Colombia comparte con Costa Rica *A. lepidior*, *A. reducta* y *P. simulans*; con Venezuela *A. bogotensis*, *A. lepidior*, *A. reducta*, *A. varia*, *P. simulans* y *S. rubra*; y con Brasil *N. entreriana* y *S. rubra*.

Se espera un aumento significativo en el número de especies y géneros registrados para Ecuador con más recolecciones en el campo y revisión de especímenes en museos regionales y nacionales. En una sola visita a Puyo, Prov. Pastaza, se encontró una alta diversidad local, cuatro especies de cuatro géneros: *I. astralis*, *M. andigena*, *Sphenorhina* sp. 2 y *Z. pubescens*.

Distribución Geográfica

Para Colombia los datos obtenidos indican que la composición del complejo salivazo varía en términos generales según la zona geográfica (Tabla 2). En el trópico bajo las especies más importantes son *A. lepidior* y *A. reducta* en las sabanas colinadas de la Costa Norte, *A. reducta* y *A. varia* en los Llanos Orientales, y *M. andigena* y *Zulia* sp. nov. en la Costa Pacífica. En las zonas interandinas predomina *Z. carbonaria* y *Z. pubescens* en el Valle geográfico del Río Cauca, y *A. reducta*, *Z. carbonaria* y *Z. pubescens* en el Magdalena Medio y Alto. Las especies predominantes en la zona andina son *M. phantastica* y *Z. pubescens*, esta última también

importante en la región del Piedemonte de la Orinoquía y Piedemonte de la Amazonía.

Los departamentos colombianos con mayor diversidad de especies registradas son Meta, Valle del Cauca y Cauca con seis especies cada uno (Tablas 3 y 4). Sin embargo, en estas regiones es donde probablemente se han hecho más recolecciones por las actividades investigativas del CIAT y CORPOICA. Es necesario realizar más recolecciones para ampliar nuestro conocimiento de la distribución geográfica en Ecuador y los 11 departamentos colombianos sin registros.

A continuación, se presenta en forma resumida para cada especie del salivazo las plantas hospedadoras registradas para Colombia, países confirmados y notas adicionales sobre la clasificación, estado de plaga y patrón de distribución. La Tabla 3 resume los departamentos colombianos donde ha sido registrada cada especie.

Aeneolamia

Aeneolamia bogotensis (Distant)

(*Tomaspis*). Hospederos registrados: ninguno. Países confirmados: Colombia, Venezuela. En Colombia *A. bogotensis* fue encontrado solamente en Cundinamarca y Meta, indicando un rango estrecho de distribución en el país, limitado a las elevaciones altas. Aunque Guagliumi (1954) afirma que anteriores registros de *A. bogotensis* para Venezuela son erróneos, se confirmó *A. bogotensis* en Venezuela (Mérida) por especímenes del MBHN. Ha sido registrado en pastos (Distant 1913), pero no hay registros de hospederos específicos en la literatura.

Aeneolamia flavilatera (Urich) (*Tomaspis*).

Una revisión de varios especímenes colombianos determinados como *A. flavilatera* en CIAT y UCOR demostró que fueron confundidos con morfo-especies de *A. varia* parecido en el patrón de color. Por eso no se pudo confirmar la presencia de *A. flavilatera* en Colombia, la cuál ha sido registrada desde Venezuela hasta Surinam (Metcalf 1961, Wiedijk 1982).

Aeneolamia lepidior (Fowler) (*Tomaspis*).

Hospederos registrados: *Brachiaria brizantha*, *B. decumbens*, *B. humidicola*, *Bothriochloa pertusa*, *Bothriochloa* sp., *Cynodon* sp., *Dichanthium aristatum*, *Digitaria decumbens*, *Melinis minutiflora*, *Panicum maximum*. Países confirmados: Colombia, Costa Rica, Panamá, Venezuela. *A. lepidior* es la segunda especie más importante en la Costa Norte de Colombia, pero su ataque es normalmente limitado a *P. maximum* y *Brachiaria* spp.; se presenta poco en *Bo. pertusa* ("colosuana"), el pasto más común en esa zona (CIAT 1999). Es la especie más ampliamente distribuida en Colombia, encontrándose en 11 departamentos.

Aeneolamia reducta (Lallemand)

(*Monecphora*). Hospederos registrados: *B. brizantha*, *B. decumbens*, *B. humidicola*, *Brachiaria* sp., *Bo. pertusa*, *Bothriochloa* sp., *D. aristatum*, *Hyparrhenia rufa*, *M. minutiflora*, *Oryza sativa*, *P. maximum*, *Pennisetum clandestinum*, *Stylosanthes* spp., y sabana nativa en general. Países confirmados: Colombia, Costa Rica, Panamá y Venezuela. *A. reducta* es la especie más importante en la Costa Norte de Colombia siendo la plaga principal de *Bo. pertusa* (Colosuana) (CIAT 1999). Ocurre en los Llanos Orientales y llega hasta el Dpto. del Tolima en el Valle del Río Magdalena, encontrándose en nueve departamentos.

Aeneolamia varia (Fabricius) (*Cercopis*).

Hospederos registrados: *B. brizantha*, *B. decumbens*, *B. humidicola*, *Brachiaria* sp., *O. sativa* y sabana nativa en general. Países confirmados: Colombia y Venezuela. *A. varia* es la plaga más abundante en los Llanos Orientales, Piedemonte de la Orinoquía y Piedemonte de la Amazonía (CIAT 1999) aunque fue registrada solamente en tres departamentos.

En Colombia *A. varia* demuestra mucho polimorfismo en patrones de color. Guagliumi describió 20 subespecies solamente para Venezuela (Guagliumi 1955) y 23 variedades fueron incluidas en el catálogo de Metcalf (1961). Uno de estos, *A. varia saccharina* (que no se conoce de Colombia o Ecuador) es la especie más reconocida por su alto impacto histórico en caña de azúcar en ciertas islas caribeñas como Trinidad (Fewkes 1969b). *A. varia (sensu lato)* está distribuido desde Colombia hasta la Guyana Francesa, Trinidad, Tobago y otras islas del sur del Caribe.

Isozulia

Isozulia astralis (Distant) (*Tomaspis*).

Hospederos registrados: *Saccharum officinarum* (en Argentina). Países confirmados: Argentina, Bolivia, Ecuador. Anteriormente conocido como *Aeneolamia astralis*, *I. astralis* fue ubicado en *Isozulia* en 1985 (Fennah 1985).

Mahanarva

Mahanarva andigena (Jacobi) (*Tomaspis*).

Hospederos registrados: *S. officinarum* (en Ecuador), *Sorghum halepense*. Países confirmados: Colombia, Ecuador. *M. andigena* fue registrada por primera vez en Colombia en la Costa Pacífica de Nariño. La misma especie fue registrada en la Costa y la Amazonía de Ecuador pero hasta ahora no ha sido registrado en la Amazonía Colombiana.

Mahanarva phantastica (Breddin)

(*Tomaspis*). Hospederos registrados: *P. clandestinum*. Países confirmados: Colombia. Esta especie es principalmente encontrada en las zonas

más altas del país a 2200 - 2600 msnm. Las bandas de color sobre el fondo negro de las alas varían desde amarillo, rojo hasta negro (sin bandas).

Mahanarva sp. nov. Hospederos registrados: *B. decumbens*, *B. dictyoneura* y *Brachiaria* sp. Países confirmados: Colombia, Ecuador. Se determinó que la especie de *Mahanarva* hallada en el Dpto. del Caquetá (Colombia) y la Amazonía y Costa de Ecuador es una nueva especie. Hasta ahora no ha sido encontrada en la Costa Pacífica Colombiana. Los machos, en particular, exhiben un amplio polimorfismo en color (Ballesteros y Gallego 1999).

Notozulia

Notozulia entreriana (Berg) (Tomaspis).

Hospederos registrados: ninguno. Países confirmados: Argentina, Brasil, Colombia, Paraguay. Existe un sólo registro de *N. entreriana* en Colombia basado en tres especímenes colectados en Carimagua, Dpto. del Meta en 1980. En Brasil, esta especie está limitada a la región central y sur del país y no ha sido registrada en los estados del norte que forman la frontera con Colombia y Venezuela (Carvalho 1995). Su registro en Colombia es curioso debido a la distancia entre el Meta y su sitio de ocurrencia en Brasil, también porque no ha sido reconocido antes o después en Carimagua a pesar estudios de campo sobre manejo y producción de forrajes por el CIAT desde 1970. La evidencia sugiere que *N. entreriana* fue introducida a Carimagua pero la población no persistió.

Prosapia

Prosapia simulans (Walker)

(*Sphenorhina*). Hospederos registrados: *Axonopus micay*, *B. decumbens*, *B. dictyoneura*, *C. plectostachys*, *Dichromena ciliata*, *H. rufa*, *S. officinarum*. Países confirmados: Belice, Colombia, Costa Rica, Honduras, México, Nicaragua, Panamá, Venezuela. *P. simulans* es una de las especies más ampliamente distribuidas en el trópico bajo, desde México hasta Panamá (Hamilton 1977). Es el primer registro del género y la especie en Suramérica. Sin embargo, se encontraron otros especímenes de *P. simulans* (CIAT) que fueron colectados en un sólo sitio en Venezuela (Estado Bolívar, La Vergareña) (Peck *et al.* en preparación).

En Colombia *P. simulans* fue detectado recientemente en cuatro sitios en el valle geográfico del Río Cauca. Se colectó en 1999 un sólo individuo en pastos de *B. dictyoneura* en el Dpto. del Cauca, Mpio. de Santander de Quilichao, a 1060 msnm. Posteriormente se localizaron tres poblaciones grandes en el Dpto. del Valle del Cauca (1) Mpio. El Cerrito, Vereda Santa Helena, 1155 msnm, (2) Mpio.

Yotoco, Vereda Cordobita, 1535 msnm, y (3) Mpio. Calima Darién, Veredas Primavera y Diamante la Esmeralda, 1621 msnm, todos en pastos de *B. decumbens*. En Calima de Darién *P. simulans* también fue reportado sobre *A. micay* y *H. rufa* (Peck *et al.* en preparación).

En Nicaragua y Honduras se conoce a *P. simulans* como uno de los cercópodos más dañinos en caña de azúcar (J. Gaviria, Centro Guatemalteco de Investigación y Capacitación de la Caña de Azúcar, CENGICANA, comunicación personal). También constituye una plaga importante en caña de Costa Rica (observación personal). Este registro conlleva implicaciones graves para la cañicultura en el Valle del Cauca. Los niveles de población encontrados en pastos de *B. decumbens* son económicamente significativos, lo cual representa una amenaza real para la persistencia de las pasturas mejoradas y la producción de leche y carne en el Valle del Cauca y otras regiones donde pudiera diseminarse (Peck *et al.* en preparación).

Sphenorhina

Sphenorhina rubra (L.) (Cicada).

Hospederos registrados: *Axonopus compressus*. Países confirmados: Brasil, Colombia, Ecuador, Guyana Inglesa, Perú, Surinam, Trinidad, Venezuela. *S. rubra* está ampliamente distribuido a través de América del Sur y es la especie de *Sphenorhina* más frecuentemente citada en asocio con gramíneas. Es una plaga ocasional de caña de azúcar en Brasil (Guagliumi 1972).

Este género diverso incluye 58 especies (Metcalf 1961), varias de las cuales utilizan gramíneas como hospedantes, pero en la mayoría los hospederos son poco conocidos. En general no se registra *Sphenorhina* por daños graves en gramíneas cultivadas fuera de *S. rubra*. En Colombia, *Sphenorhina* sp. 1 fue encontrado en *P. clandestinum* en el Cauca. *Sphenorhina* sp. 2 (de Ecuador) fue asociado con gramíneas al lado de caña de azúcar.

Zulia

Zulia birubromaculata (Lallemand)

(*Monecphora*). Hospederos registrados: *Cestrum* sp. ("tintillo"). Países confirmados: Colombia. Hasta ahora esta especie no ha sido registrada fuera de Colombia. No conocemos ninguna observación o publicación de ella como plaga importante. En Colombia ha sido registrado en los Dptos. de Nariño y Valle del Cauca en la Costa Pacífica.

Zulia carbonaria (Lallemand)

(*Monecphora*). Hospederos registrados: *Andropogon gayanus*, *B. brizantha*, *B. decumbens*, *B. dictyoneura*, *B. humidicola*, *Brachiaria plantaginea*, *Brachiaria* sp., *Cynodon* sp., *D. decumbens*, *O. sativa*, *P.*

clandestinum, *S. officinarum*. Países confirmados: Bolivia, Colombia. Desde hace 20 años *Z. carbonaria* ha sido conocido en Colombia como *Z. colombiana* (Arango y Calderón 1981, Calderón *et al.* 1982, Ospina *et al.* 1985, Chávez *et al.* 1990, Arango 1991), el cuál representa una determinación errada ya que se distingue fácilmente del holotipo de *Z. colombiana*. Además, el nombre *Z. colombiana* es un sinónimo menor de *Z. pubescens*, así que debe ser retirado su uso. *Z. carbonaria* se distingue de *Z. pubescens* por su mayor tamaño y particularmente por el perfil de rostro redondo en vez de angulado.

Z. carbonaria fue encontrada en seis departamentos colombianos. Su registro en el Dpto. del Caquetá es curioso por estar apartado al resto del rango de distribución. Además, su distribución en Caquetá parece ser muy localizada. *Z. carbonaria* fue encontrada solamente en 3 de 9 sitios en Caquetá donde se hicieron recolecciones varias veces en los años 1998-1999. Constituyó 17.0, 0.3 y 0.1% de la composición de especie en los tres sitios ubicados en los municipios de La Montañita (Fca. La Rueda), San José del Fragua (Fca. El Diamante) y Florencia (Hda. Durania), respectivamente (Puentes y Ramírez 1999, Blanco y Giraldo 1999). Vale la pena señalar que el material vegetal de *Brachiaria* fue introducido durante los últimos 15 años a La Rueda desde el Dpto. del Cauca, Mpio. de Santander de Quilichao (G. Ruiz, Universidad de la Amazonía, comunicación personal) donde *Z. carbonaria* es la especie predominante. Aunque no se puede probar que *Z. carbonaria* invadió al Caquetá por material infestado, subraya la importancia de ejercer un mejor manejo sobre el traslado de material vegetal. Los huevos de *Z. carbonaria* son puestos en la superficie del suelo pero también en la hojarasca y se pega a la superficie del tallo inferior (Rodríguez *et al.* 2000).

Zulia pubescens (Fabricius) (Cercopis).

Hospederos registrados: *Axonopus scoparius*, *B. brizantha*, *B. decumbens*, *B. dictyoneura*, *B. humidicola*, *Brachiaria* sp., *Calopogonium* sp., gramíneas nativas, *Homolepsis aturensis*, *Homolepsis* sp., *O. sativa*, *P. maximum* y *P. clandestinum*. Países confirmados: Colombia, Ecuador, Guyana Francesa, Guyana Inglesa, Perú, Surinam, Trinidad. *Z. pubescens* fue registrada en 10 departamentos y por el rango de hábitats que ocupa es probablemente la especie más ampliamente distribuida en el país. Ocurre desde la Cordillera Occidental hasta el Piedemonte de la Amazonía y al norte hasta el Dpto. de Antioquia.

Zulia sp. nov. Hospederos registrados: *Brachiaria mutica*. Países confirmados: Colombia, Ecuador. Esta especie de *Zulia* hallada en la costa del Dpto. de Nariño y las Provincias de Esmeraldas y Pichincha en Ecuador fue determinada como una

nueva especie. Aunque es parecido a *Z. pubescens* en tamaño, es café oscuro/negro claro en vez de negro oscuro y tiene el perfil de rostro redondo.

Implicaciones

A pesar del alto nivel comparativo de la investigación en Colombia sobre el salivazo de los pastos, se han obtenido registros de nuevas especies y nuevos rangos de distribución. Es urgente realizar más recolecciones tanto en Colombia como en Ecuador con el fin de describir el complejo de salivazo en las regiones donde todavía este es desconocido y documentar la diversidad regional actual. Estos inventarios servirán para vigilar el traslado o introducción de especies y la emergencia de nuevas plagas. Unas regiones claves son el Chocó Geográfico, la Costa Pacífica y la Amazonía Colombiana que están contiguas a regiones diversas del trópico bajo y donde se han encontrado nuevas especies.

Prosapia simulans en Suramérica, *N. enteriana* en los Llanos Orientales y *Z. carbonaria* en el Piedemonte de la Amazonía puedan representar introducciones o invasiones desde Centroamérica, Brasil y el Dpto. del Cauca respectivamente. Esta evidencia sugiere que la introducción de especies exóticas de salivazo es un riesgo ya que amenazan la producción de forrajes y caña de azúcar en los nuevos hábitats.

Es necesario hacer recolecciones de más datos sobre la distribución del salivazo, analizarlos en forma más detallada, y construir un mapa de rango de distribución para las especies colombianas con el fin de empezar a interpretar los patrones de distribución y guiar un estudio sobre los determinantes de distribución. Para cercopidos, estas determinantes son desconocidas en su mayoría. La evidencia en este estudio preliminar demuestra variación taxonómica en la flexibilidad de la distribución. Por ejemplo, si se consideran los registros de *Z. pubescens* con información de elevación, esta especie ocurre a 250-450 msnm en el Piedemonte de la Amazonía (Dpto. del Caquetá) pero en el Valle geográfico del Río Cauca normalmente ocurre por encima de los 1400 msnm hasta 2265 msnm en el Dpto. de Antioquia. *A. reducta* está aparentemente limitada hasta los 300 msnm en la Costa Norte y los Llanos Orientales del país pero en el Valle del Río Magdalena Medio y Alto (Dpto. del Tolima) se obtuvieron dos registros a 1300 msnm.

Dada la variación intraespecífica y convergencia interespecífica exhibida por muchas especies, las estructuras de la genitalia del macho son las características más importantes para distinguir especies. Sin embargo a nivel geográfico debe ser posible establecer claves de diagnóstico basados en

forma, tamaño y coloración de los adultos. Determinaciones taxonómicas correctas y la ubicación de especímenes vouchers en colecciones de museos son prioritarias para aumentar el impacto de la investigación.

Las estrategias del manejo del salivazo en las regiones donde tiene importancia económica deben estar formuladas para el complejo específico local ya que existe bastante variación entre las especies en términos de biología y ecología. La región misma influye en la ecología presentada por las especies. En el Piedemonte de la Amazonía, por ejemplo, no hay una estación seca marcada, la cuál hace que el desarrollo poblacional no sea sincronizado (CIAT 1999). Al contrario, las poblaciones son mucho más sincronizadas en sitios estacionales como la Costa Norte y el Piedemonte de la Orinoquía.

Conclusiones

- En Colombia, se encontraron 15 especies de 7 géneros del salivazo de los pastos registrados mediante examinación de especímenes en museos y observaciones de campo. Un examen preliminar para Ecuador confirmó nueve especies de cuatro géneros. Seis especies son comunes para ambos países.
- Se descubrió un cambio mayor en la nomenclatura del grupo. Lo que anteriormente se conocía como *Z. colombiana* en Colombia es en realidad *Z. carbonaria*. Además, *Z. colombiana* es un sinónimo menor de *Z. pubescens* y por esta razón se debe retirar su uso.
- Dos especies fueron determinadas como nuevas: *Mahanarva* sp. nov. en el Piedemonte de la Amazonía del Dpto. del Caquetá (Colombia) y Ecuador, y *Zulia* sp. nov. en la Costa Pacífica del Dpto. de Nariño (Colombia) y Ecuador.
- Se obtuvieron nuevos datos de diversidad y distribución incluyendo *Z. carbonaria* en el Piedemonte de la Amazonía; *Mahanarva andigena*, *Mahanarva* sp. nov., *Notozulia entreriana* y *Zulia* sp. nov. para Colombia y *Prosapia simulans* para Suramérica. Se reporta por primera vez el género *Prosapia* en Suramérica.
- La presencia de *P. simulans* en el Valle Geográfico del Río Cauca merece una especial atención ya que esta especie es una de las plagas más importantes en caña de azúcar para ciertas regiones de Centroamérica.
- Las gramíneas cultivadas o silvestres registradas como hospederos para el salivazo en Colombia y Ecuador son: *Andropogon gayanus*, *Axonopus compressus*, *A. micay*, *A. scoparius*, *Brachiaria plantaginea*, *B. brizantha*, *B. decumbens*, *B.*

dictyoneura, *B. humidicola*, *B. mutica*, *Bothriochloa pertusa*, *Bothriochloa* sp., *Calopogonium* sp., *Cestrum* sp., *Cynodon plectostachys*, *Cynodon* sp., *Dichanthium aristatum*, *Dichromena ciliata*, *Digitaria decumbens*, *Homolepsis aturensis*, *Hyparrhenia rufa*, *Melinis minutiflora*, *Oryza sativa*, *Panicum maximum*, *Pennisetum clandestinum*, *Saccharum officinarum*, y *Sorghum halepense*.

- Es urgente realizar más recolecciones del complejo de las especies de salivazo en Colombia y Ecuador para ampliar los conocimientos del grupo y poder identificar nuevas plagas inmigrantes o invasoras. En Colombia las áreas críticas son el Chocó Geográfico, Costa Pacífica y Amazonía.
- Los datos obtenidos muestran que el rango de distribución varía entre especies y que diferentes regiones geográficas aportan un complejo distinto. Es importante considerar esta variación para guiar avances en el manejo mediante estudios bioecológicos y tácticas de control dirigidos a las especies locales.

Agradecimientos

Quiero agradecer los esfuerzos de G. Arango quien contribuyó con 135 registros de distribución, S. Lapointe (39), C. García (20) y R. Maldonado (15). Para el acceso a las colecciones de museo se agradece a P. Hernández (CIAT), R. Hoebeke (UCOR), N. C. Mesa (UNP) y particularmente M. Webb (MBHN) por el permiso de examinar los especímenes tipos. C. Medina (Universidad de Pretoria, Sudáfrica), N. C. Mesa (Universidad Nacional sede Palmira) y B. Arenas (CIAT) hicieron comentarios detallados sobre el manuscrito. F. López, J. Rodríguez, U. Castro y A. Morales (CIAT) ayudaron en varias etapas de la preparación del manuscrito. Este estudio fue realizado con la ayuda financiera de la Organización de los Estados Americanos, Nestlé de Colombia, y el Fondo Nacional del Ganado en Colombia.

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Tabla 1. Diversidad y distribución de especies de salivazo en gramíneas de Ecuador

Especie	Provincias	Zona geográfica	
		Amazonía	Costa
<i>Isozulia astralis</i>	Pastaza	X	
<i>Isozulia minor</i> (christenseni) ¹	Napo	X	
<i>Mahanarva andigena</i>	Chimborazo, Esmeraldas, Guajas, Pastaza, Tungurahua	X	X
<i>Mahanarva phantastica</i> ¹	Tungurahua		
<i>Mahanarva</i> sp. nov.	Napo, Pichincha, Sucumbios	X	X
<i>Sphenorhina rubra</i>	Napo	X	
<i>Sphenorhina</i> sp. 2	Pastaza	X	
<i>Zulia pubescens</i>	Cotopaxi, Napo, Pastaza, Pichincha, Sucumbios, Tungurahua	X	
<i>Zulia</i> sp. nov.	Esmeraldas, Pichincha		X

¹Citado de la literatura no por especímenes examinados (*I. minor*: Metcalf 1961, Fennah 1985; *M. phantastica*: Goding 1923)

Tabla 2. Principales especies del complejo salivazo según zona geográfica de Colombia.

Región	Especies principales
Costa Norte	<i>A. lepidior</i> , <i>A. reducta</i>
Costa Pacífica	<i>M. andigena</i> , <i>Z. pubescens</i> , <i>Zulia</i> sp. nov.
Llanos Orientales	<i>A. varia</i> , <i>A. reducta</i>
Magdalena Medio/Alto	<i>A. lepidior</i> , <i>A. reducta</i> , <i>Z. carbonaria</i> , <i>Z. pubescens</i>
Piedemonte de la Amazonía	<i>A. varia</i> , <i>Mahanarva</i> sp. nov., <i>Z. carbonaria</i> , <i>Z. pubescens</i>
Piedemonte de la Orinoquía	<i>A. varia</i> , <i>A. reducta</i> , <i>Z. pubescens</i>
Valle Geográfico Río Cauca	<i>P. simulans</i> , <i>Z. carbonaria</i> , <i>Z. pubescens</i>
Zona Andina	<i>A. bogotensis</i> , <i>M. phantastica</i> , <i>Z. pubescens</i>

Tabla 3. Diversidad y distribución de especies de salivazo en gramíneas según departamento colombiano.

Especie	Departamento colombiano														
	Ama	Atl	Bol	Boy	Cal	Caq	Cas	Cau	Ces	Cór	Cun	Mag	Met	Nar	Qui
<i>A. bogotensis</i>	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-
<i>A. lepidior</i>	-	X	X	-	X	-	-	X ¹	X	X	-	X	-	X	-
<i>A. reducta</i>	-	X	X	-	-	-	-	-	X	X	-	X	X	X	-
<i>A. varia</i>	-	-	-	-	-	X	-	-	-	-	-	-	X	-	-
<i>M. andigena</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>M. phantastica</i>	-	X	-	-	X	-	-	X ²	-	-	-	-	-	-	X ²
<i>Mahanarva</i> sp. nov.	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-
<i>N. entreriana</i>	-	-	-	-	-	-	-	-	-	-	-	-	X ²	-	-
<i>P. simulans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
<i>S. rubra</i>	-	-	-	-	-	-	-	-	-	-	-	-	X ²	-	-
<i>Sphenorhina</i> sp. 1	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
<i>Z. birubromaculata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	X ²	-
<i>Z. carbonaria</i>	-	X	-	-	X	X	-	X	-	-	-	-	-	-	X
<i>Z. pubescens</i>	X ²	X	-	X ¹	-	X	-	X	-	-	-	-	X	X	-
<i>Zulia</i> sp. nov.	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-

¹Isla de Gorgona²Un sólo registro

DESIGN AND MANAGEMENT OF A NEW SMALL-SCALE REARING UNIT AND IMPROVED MASS-REARING COLONY FOR GRASSLAND SPITTLEBUGS (HOMOPTERA: CERCOPIDAE)

sometido a:

Journal of Economic Entomology

DANIEL C. PECK, ANUAR MORALES, AND ULISES CASTRO

Centro Internacional de Agricultura Tropical (CIAT), Apartado Aéreo 6713, Cali, Colombia

Resumen. Two rearing technologies for neotropical grassland spittlebugs are described and evaluated with *Aeneolamia varia* (F.) on *Brachiaria ruziziensis* Germ. & Evrard. First, a new small-scale rearing unit was developed as a tool for maintaining spittlebug life stages in the greenhouse throughout the year in order to promote biological studies. This unit features a plant tray established with roots as feeding sites for nymphal development alongside an adult emergence cage with oviposition substrate and food plants for egg collection. Secondly, an improved mass-rearing colony based on recent advances in spittlebug rearing techniques was designed to reduce inputs and streamline production. The major feature was a covered box with high quality root and microclimate conditions for nymphal development. Efficiency of adult production from eggs was 45.1%, yield 1002 adults/m², nymphal development time 36.1 d, and adult emergence 70.5% in a 1-wk period. The improved mass-rearing design is a more effective tool for reliable and high-level production of spittlebugs for massive screening required for the evaluation of control tactics such as fungal entomopathogens and host plant resistance. The possibilities for further improving these designs and tailoring them to other spittlebug species is discussed.

KEY WORDS *Aeneolamia varia*, *Brachiaria*, forage grass pest, froghopper, rearing technique

GRASSLAND SPITTLEBUGS (Homoptera: Cercopidae) continue to pose one of the most challenging biotic limits to forage grass, milk and beef production in rangelands and pastures of the Neotropics. These native pests damage most improved forage grasses such as the widely sown and highly susceptible *Brachiaria decumbens* Stapf, an African grass well-adapted and highly productive under the acid and infertile conditions of the humid and subhumid tropics (Keller-Grein et al. 1996). Other species from forage grass genera such as *Cenchrus* (Enkerlin & Morales 1979), *Cynodon* (Taliaferro et al. 1967, Fagan & Picado 1971), *Panicum* (Thomas & Lapointe 1989), and *Pennisetum* (Peck 1998) are highly injured by this pest complex as is sugar cane (*Saccharum officinarum* L.) (Fewkes 1969) and under certain circumstances rice (*Oryza sativa* L.) (Nilakhe 1985, Souza & Nilakhe 1985).

Although regional economic damage due to spittlebugs has been only superficially assessed, quantitative impact studies on some spittlebug/forage combinations have documented a very significant negative effect on the yield and quality of forage, and consequently on the establishment and persistence of improved pastures (Valério & Nakano 1987, 1988, 1989). In susceptible forage grasses, severe outbreaks cause die-back of all the above-ground biomass thereby promoting weed invasion and contributing to environmental degradation.

A particular challenge to management of this pest complex is its diversity. Dozens of species

from at least 11 genera attack graminoids in the New World (D.P., unpublished data). The group achieves pest status under widely varying habitats ranging from the southern United States to southern Brazil, extensive to intensive grazing systems, lowlands to highlands, and in regions that are continuously humid to highly seasonal in precipitation. Outbreaks of spittlebugs are increasing in certain regions such as hillsides and forest margins of Colombia, pastures of northern Argentina, and sugar cane of Central America and Ecuador.

The biology and ecology of most economically important spittlebugs have never been studied. Advances in management thereby suffer from ineffective tailoring of control tactics to local species composition and habitat conditions. One limitation is the lack of appropriate methodologies for maintaining small-scale colonies in the greenhouse to support studies by research groups that have limited personnel and other resources. In addition, biological studies should be encouraged in the insect's natural range. Anecdotal evidence for the introduction of spittlebug species to new regions argues against inappropriate transfer of pest spittlebugs from one geographic zone to the next due to risks of new pest introductions (Peck et al. in prep.).

For research groups with greater capacity, mass-rearing spittlebugs is a necessary tool for evaluation of control techniques. As methodologies improve for the evaluation of fungal

entomopathogens (CIAT 1999) and the screening of germplasm for host plant resistance (Cardona et al. 1999), throughput is increasingly dependent on a reliable, continuous and high-level production of eggs, nymphs and adults. Streamlining the rearing methodology will help achieve these requirements as well as increase efficiency and reduce inputs of materials, labor and space.

Earlier techniques for rearing grassland spittlebugs have confronted particular challenges including the adequate preparation of roots for nymphal feeding sites, maintenance of high humidity for nymphal development, and efficient recovery of eggs from oviposition substrate. Fewkes & Demidecki-Demidowicz (1971) reared *Aeneolamia varia saccharina* (Distant) and *Aeneolamia postica jugata* (Fowler) on roots of maize plants that perforated fibrous pots bedded onto plant nutrient solution; moist filter paper served as oviposition substrate. McWilliams & Cook (1975) reared nymphs of *Prosapia bicincta* (Say) on pearl millet grown in vermiculite with commercial plant food and obtained eggs from cotton oviposition substrates. Pacheco & Silva (1982) obtained 27.9% survivability of *Deois flavopicta* (Stål) nymphs reared on uprooted clumps of *Brachiaria plantaginea* (Link) Hitchc. kept in glass beakers with water. Neto & Pavan (1984) achieved 48–100% survivability of *Deois* sp. nymphs simply grown on potted *Digitaria decumbens* Stent held in a water tray under protective screen cages to maintain high humidity. Magalhães et al. (1987) raised nymphs of *Deois incompleta* (Walker) on potted *Brachiaria humidicola* (Rendle) Schweik. and used filter paper as an oviposition substrate.

Lapointe et al. (1989) is the most recent report of an improved mass-rearing technique. A key characteristic of their methodology was establishment of favorable conditions for nymphal development featuring abundant surface roots and high humidity in pots covered by aluminum lids. The second major advance was preparation of a soil oviposition substrate that permitted efficient recovery of eggs through sieving and decanting. Although efficiency was not reported, current work with this traditional methodology at CIAT using *Aeneolamia varia* (F.) produces an efficiency of approximately 50% (adults from eggs) and overall yield of 800 adults/m² (R. Pareja, CIAT, personal communication). Finally, Cruz et al. (1997) evaluated a new technique for nymphal rearing that essentially reproduced the high humidity conditions and surface root availability of the pot in a larger box environment thereby reducing soil, space and pot requirements. Although only evaluated on a small scale, this technique showed

promise for integration into an improved mass-rearing colony.

Here we report on two advances in spittlebug rearing technologies. The first is a new small-scale rearing unit. We sought to develop a unit that met several general characteristics: adaptability to a variety of spittlebug species and genera; low labor, space and time requirements for operation by small research groups; and effective maintenance of all life stages year round to promote continued studies on biology despite the absence of the insect in the field during the dry season. An important component of our design strategy was to combine nymphal rearing and egg laying chambers thereby eliminating a major bottleneck in the traditional mass-rearing colony used by CIAT.

The second is an improved mass-rearing facility to support studies on fungal entomopathogens and host plant resistance where a large, dependable, year-round source of eggs, nymphs and adults are required for evaluations. We implemented and evaluated a new mass-rearing technique that integrated recent advances built on years of experience at CIAT where the Tropical Grasses and Legumes Project has been raising spittlebugs for studies on host plant resistance for more than 15 years. The objective was to establish a reliable and more economical methodology for mass production of spittlebug eggs and adults.

Materials and Methods

Insect and Plant Material

Both rearing techniques were developed and evaluated with the spittlebug *A. varia*. This species was chosen because it is the most damaging cercopid in the extensive Eastern Llanos and the Amazonian Piedmont of Colombia. CIAT also has >15 years of experience managing a screenhouse colony of this species. All *A. varia* used in the present study were obtained from this long-established colony that is periodically reinvigorated with insects from the field and managed with the traditional methodology of Lapointe et al. (1989).

All plant material was *Brachiaria ruziziensis* Germ. & Evrard (CIAT accession 0654) obtained from field plots at CIAT's campus, Palmira, Valle del Cauca, Colombia. *B. ruziziensis* was chosen because it is an acceptable host and is easier to manage in the screenhouse than *B. decumbens*, being more responsive to planting conditions and establishment of secondary roots for nymphal feeding.

Rearing Unit

The oviposition component of the unit was built around a frame of aluminum posts (height 48

cm) (Fig. 1). Legs of the posts were placed in water dishes to exclude ants. Plant trays (61.0 x 30.6 x 3.4 cm l/w/h) were fitted at two levels (16 and 46 cm). The frame was wrapped on the outside between the two levels with a sheet of shade cloth to form walls that reduced light, elevated humidity and prevented escape of the insects. Stems of potted host plant (*B. ruziziensis*) entered the unit through lateral slits in the nylon at two sides to provide adults with food. A tray with specially prepared soil oviposition substrate was fitted in the bottom level while the top was covered by either a plant tray that served as a lid or one that was prepared with roots that housed late instars. The oviposition substrate and egg extraction techniques were identical to those described in Lapointe et al. (1989). The soil oviposition substrate with eggs was washed in water and passed through a series of sieves to remove particulates, followed by egg extraction using flotation in a saline solution.

Plant trays were specially prepared to provide feeding and development sites for nymphs. The entire bottom of each plant tray was perforated with holes that allowed roots to descend. Trays were planted with 21 *B. ruziziensis* plants (comprising 5–7 stems each) in a 2 cm layer of soil. The best root growth was obtained by using young material with partially pruned roots and foliage and planted in contact with the bottom of the tray in soil fertilized with N:P:K at 2 g/l water. After 5 d this tray was stacked on top of another with a dusting of fertilized soil to stimulate root growth. The space between the trays filled with roots adequate for infestation with eggs about 3 wk after transplantation. Trays were infested with 500 eggs 1–2 d before eclosion. The eggs, in groups of 50 on pieces of cut filter paper, were placed on the lower tray with the upper tray of roots replaced on top.

Three weeks after infestation the tray was mounted upon a wooden frame (58 x 29 x 10 cm l/w/h) (Fig. 2). This frame permitted the roots to descend and give the adults more space to emerge. The dark and high humidity conditions helped to maintain root quality. Before emergence of the adults this frame was connected to the aluminum oviposition chamber. Adults moved toward the relative light of the oviposition chamber through a slit (1.5 x 56.0 cm) along the abutting long side of the wooden frame.

We evaluated three versions of the rearing unit for sex ratio of emerging adults, and for efficiency, measured as the proportion of infested eggs that emerged as adults. The first version was the complete unit as described above where adults were recovered from the oviposition chamber after emerging from the wooden frame where nymphs completed development. We tested a second version

thought to increase emergence from the dark conditions under the wooden frame by allowing adults to emerge into a higher light environment. This consisted of just the nymphal rearing unit where adults left the wooden frame through the same slit but into an emergence cage (61.5 x 31.0 x 30.0 cm l/w/h) covered in white nylon no-see-um netting. The third version was as the unit was originally conceived, consisting of a single unit where the root tray with nymphs was placed on top of the oviposition chamber 3 wk after infestation without use of the wooden frame; this gauged the capacity of roots that were more exposed to support nymphal development and adult emergence.

Six paired repetitions of versions 2 and 3 were evaluated on separate dates from October 1997 to February 1998 whereas five repetitions of version 1 were evaluated subsequently from August 1998 to June 1999. Differences in adult sex ratio and efficiency among these three versions were tested using the Tukey-Kramer HSD test while deviations from a 1:1 sex ratio were tested using the Wilcoxon signed-rank nonparametric test (SAS Institute 1989).

Improved Mass-Rearing Colony

Plants of *B. ruziziensis* were brought from the field, washed, partially pruned of roots and foliage, as above, and planted into 750 cm³ pots. After 2 wk, 16 plants were transplanted to the nymphal rearing box that comprised a wooden frame (120 x 60 x 10 cm l/w/h) with a 4–5 cm soil layer on the bottom. Roots of the transplants (5–7 stems each) were placed onto small mounds of soil. These were covered with perforated inverted pots to promote root growth and improve anchoring of the plant to the substrate. After 1 wk, the pots were removed, and the box was covered with a double layer of cloth formed of black polyester shade cloth below and white cotton material above. Stems and foliage emerged from 16 openings in the cloth. This arrangement provided dark and humid conditions that stimulated the continued development of roots down the mounds of soil. These surface roots are required by early instars for feeding sites and are therefore one of the most critical steps in the rearing process (Fig. 3).

Immediately after covering the box with the cloth, plants were infested with eggs of *A. varia* 1–2 d before eclosion. Eggs were applied in groups of 50 on pieces of moist filter paper placed near the roots. Applications of urea (2%) were made 4 and 6 wk after transplantation from the field and plants were watered as required with care taken not to wash away eggs or spittle masses. Four to 5 wk after infestation or at first adult emergence, an emergence cage (120 x 60 x 60 cm l/w/h) was placed over the

box to prevent escape. Adults were collected daily with an aspirator from the foliage and from the rooting area below the cloth. Those adults not required for screening tests were transferred to oviposition cages for the collection of eggs. Nymphal rearing boxes and adult oviposition chambers were protected from ants by placing the feet of their supporting tables in dishes filled with water.

To measure the efficiency of adult production from eggs, two boxes were infested each week over 32 consecutive weeks from 17 July 1998 to 15 March 1999 with the exception of three weeks when shortage of eggs prevented infestations. Two egg infestation levels were evaluated: 100 eggs per plant, or a total of 1600 eggs per box ($n=16$), and 150 per plant, or a total of 2400 per box ($n=13$). We also measured the success of egg hatch under these conditions to gauge how efficiency depended on egg mortality. During five consecutive generations a subsample of eggs (approximately 800) were placed on moist filter paper and divided among four petri dishes situated in the corners of the box. Hatching success under the colony conditions was compared with another group kept under ideal incubation conditions (darkness, 27°C, 100% RH). A two-sample t-test was used to evaluate differences in efficiency and total adult production between the two infestation levels, and to evaluate egg mortality between the two hatching conditions.

Results

Rearing Unit

Use of the wooden frame significantly increased efficiency of adult emergence from eggs (Table 1). About 2.1 times more adults were obtained when nymphs and their roots were kept under the conditions inside the wooden frame (version 2; adults exited into the white emergence cage) than when nymphs and roots were placed at the top of the oviposition chamber under more exposed conditions (version 3). This could be explained by direct or indirect effects on nymph survivorship. Higher humidity may have favored spittle mass maintenance. In addition, increased darkness and higher humidity may have enhanced root vigor and quality and/or maintained these characteristics for a longer period of time during the relatively long development period of nymphs. When exposed at the top of the oviposition chamber, roots visibly deteriorated and senesced more rapidly than on the wooden frame. Maintaining healthy roots for nymphal feeding is therefore a critical component of successful rearing.

Adults were able to exit the dark nymphal rearing chamber through a slit in the wooden frame

towards the light of the emergence cage. Sixty percent of eggs successfully hatched, completed nymphal development and exited the wooden box (version 2). Efficiency, however, was significantly reduced to 18.9% when adults emerged into the oviposition chamber (version 1; Table 1). From these data we infer that the reduced light in the oviposition chamber (walled with black shade cloth) did not attract adults as effectively as the emergence cage (walled with white netting). Versions 1 and 3 did not differ in efficiency, suggesting that although the wooden frame might enhance nymph survivorship through root maintenance, the advantage is counterbalanced by adults unsuccessful in exiting to the oviposition chamber.

Among the three versions evaluated the male:female sex ratio varied from 1.05 to 1.24 but no statistically significant differences were detected. For each of the three versions, adult sex ratio did not differ from 1:1 ($\text{Prob}>|t|=0.62, 0.44, 0.16$ for versions 1, 2 and 3 respectively).

Improved Mass-Rearing Colony

Adults from each generation emerged over a period of approximately 2 wk due to differences in individual development times (Fig. 4). The first adult collection date represented the accumulation of individuals over 2–4 d. However, 70.5% of adults emerged within the 7 d after this first collection date, an acceptable level of population synchrony especially if eggs are collected weekly to initiate a new generation.

Mean time to median adult emergence was 36.10 ± 0.54 d (31–47). Mean time from egg infestation to first and last adult emergence was 31.59 ± 0.49 d (25–41) and 40.62 ± 0.69 d (35–60), respectively.

Efficiency varied widely throughout the beginning of the study (weeks 1–20) as adjustments were made and the rhythm of management was established (Fig. 5). Mean efficiency during this period was $28.40 \pm 2.81\%$ (13.67–55.81). In the last third of the study (weeks 21–28) efficiency stabilized to a mean of $45.11 \pm 1.07\%$ (35.94–51.56). During this last period, a mean of 1002 ± 23.8 adults/m² (798.6–1145.8) was produced.

For infestation levels of 100 and 150 eggs per plant, the mean number of adults produced per box was 601 and 678, respectively, but no significant difference was detected (t-test, $df=56$, $P>0.1$). Efficiency, however, did differ between infestation levels. Efficiency was $37.56 \pm 2.01\%$ (9.0–51.56) for 100 eggs per plant but only $28.70 \pm 2.70\%$ (4.75–64.75) for 150 eggs per plant (t-test, $df=56$, $P<0.01$).

There was no difference in the eclosion success of eggs under conditions of the colony or

incubation (t-test, $df=8$, $P>0.9$). Mean hatching success was $90.85 \pm 2.35\%$ (81.28–97.37) and $90.39 \pm 2.81\%$ (77.88–96.69) for the colony and incubation, respectively. The conditions of the colony were therefore optimal for the successful emergence of first instars.

Discussion

The rearing unit offers an alternative for small research groups addressing the biology of different spittlebug species through in situ studies. With minor modifications the rearing unit should be practical and effective for maintaining life stages of different grassland spittlebug species and genera year round. The unit is low cost (US\$40–50), requires little space (0.5 m^2) and management, and produces an even sex ratio. Efficiency of 25% (adult production from eggs in versions 1 and 3) is sufficient for this style of colony but advances in efficiency could be achieved through more effective manipulation of root quality, number of eggs infested, and light conditions. Evidence that adults can be attracted from nymphal sites to oviposition sites due to light gradients should be considered as a technique to integrate into mass-rearing where a major bottleneck is the manual collection and transfer of new adults.

This improved mass-rearing colony is a more effective tool than the traditional CIAT colony for massive screening required in studies of host plant resistance and fungal entomopathogens. The improved design requires less space, soil and labor, yet maintains a similar efficiency. Production of 1002 adults/ m^2 is about 1.25 times the production obtained by the traditional colony. About 15 person-hours are required per week to maintain two boxes, but economy of scale would allow a doubling of adult production with 5 additional hours a week, largely dedicated to transplanting material from the field. With practice, the variation in adult production from one cohort to the next is low, thereby ensuring a continuous and dependable supply of insects for evaluation. Adult emergence is sufficiently synchronous that in a single week period 70.5% emerge. Variation in development time could depend in part on temperature because lower night temperatures appeared to correspond with longer nymphal development.

An additional advantage is the emergence cage that facilitates capture of new adults and decreases the risk of greenhouse escape by imposing two barriers to the outside environment. The improved design may also suffer less from pests, diseases and other contamination. Over a 1-yr period the traditional colony experienced several isolated

outbreaks of fungal entomopathogens, whereas the improved colony experienced none. The particular temperature and humidity conditions of the covered pots housing nymphs in the traditional colony may be better for propagation of pathogens. Other occasional pest problems included toads, spiders and earwigs; ants were largely excluded when legs of the tables were put in water traps.

The time of nymphal development is only 2–4 d longer than the traditional method. Biological studies carried out under the conditions of the traditional pot method showed a mean nymph duration of 30.8 d for *A. varia* (Diaz 1999) compared to 36.1 d in the improved design which included the 1–3 d for eclosion after infestation. It is expected that certain minor modifications would be required to tailor this improved methodology to other species of grassland species. *Zulia carbonaria* (Lallemand), for example, is more than twice the size of *A. varia* and should be infested at lower rates to obtain the highest efficiency. Variations of the rearing unit, and the traditional and improved mass-rearing designs have already been used successfully at CIAT for additional Colombian species including *Mahanarva andigena* (Jacobi), *Mahanarva* sp. nov., *Prosapia simulans* (Walker), *Z. carbonaria*, *Zulia pubescens* (F.) and *Zulia* sp. nov.

In the mass-rearing colony, increasing the efficiency of production depends on fine-tuning levels of egg infestation and adjusting fertilizer additions in consideration of host plant deterioration. Elevating egg infestation from 100 to 150 per plant did not increase overall adult production significantly but did decrease the efficiency of adult production. Under the high infestation level, plant vigor was drastically reduced by the time nymphs developed to fifth instars and many individuals were left to wander apparently without adequate feeding sites. We found that fifth instars quickly and successfully established on fresh plant material when the most damaged 1–2 plants were replaced with new plants removed from their pots. Late instars of *A. varia* perform well at the base of plant stems rather than roots so the new material appeared to increase survivorship until production of the teneral spittle mass and emergence of the adults. Additional gains in efficiency could be obtained through improved infestation techniques that more evenly distribute eggs on the available roots. A promising technique is temporarily drying eggs and applying them to the base of the host plant with a salt shaker or other applicator with small holes (R. Pareja, CIAT, personal communication).

A major bottleneck that remains in streamlining the mass-rearing is the collection of adults for transfer to oviposition chambers. Although adults can be collected much more efficiently from

under a single emergence cage in the improved design, rather than from many individual pots as in the traditional design, it is still a laborious process. Continued improvements in spittlebug mass-rearing will therefore include features such as (1) light gradients to lead adults from nymphal development sites to oviposition sites, (2) a technique to evenly distribute eggs onto the soil and roots, (3) a protocol to terminate egg diapause thereby utilizing the proportion of eggs that are discarded because of delayed development, and (4) any other technique to increase the rate and synchrony of development.

Acknowledgements

We especially thank R. Pareja (CIAT) for his generous contribution of experience and expertise to every stage of this study. F. López (Universidad del Valle) and J. Rodríguez (Universidad del Tolima) gave assistance during many phases; A. López and M. González (Universidad del Tolima) were instrumental for initial establishment of the mass-rearing colony; G. Sotelo and M. Cruz (CIAT) offered critical advice. This research was partially funded by the Fondo Nacional de Ganado (FEDEGAN, Colombia), a PRG Fellowship from the Organization of American States awarded to D.P. and the Young Researcher's Fellowship from the Instituto Colombiano para el Desarrollo de la Ciencia y la Tecnología (COLCIENCIAS, Colombia) awarded to U.C.

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Table 1. Production of adults (mean $\pm$ SE [range]) from 500 eggs of *A. varia* in three versions of the small-scale rearing unit

Version	n	Adults recovered	Efficiency	Male:female sex ratio
Version 1 (Complete unit)	5	94.4 $\pm$ 14.81a (48–134)	18.9 $\pm$ 2.96a (9.6–26.8)	1.05 $\pm$ 0.097a (0.77–1.09)
Version 2 (Wooden frame)	6	299.8 $\pm$ 26.70b (220–372)	60.0 $\pm$ 5.34b (44.0–74.4)	1.06 $\pm$ 0.049a (0.88–1.22)
Version 3 (Oviposition chamber)	6	142.3 $\pm$ 25.09a (51–232)	28.5 $\pm$ 5.02a (10.2–46.4)	1.24 $\pm$ 0.118a (0.77–1.55)

Within columns, values with different letters are statistically different ($P < 0.05$)

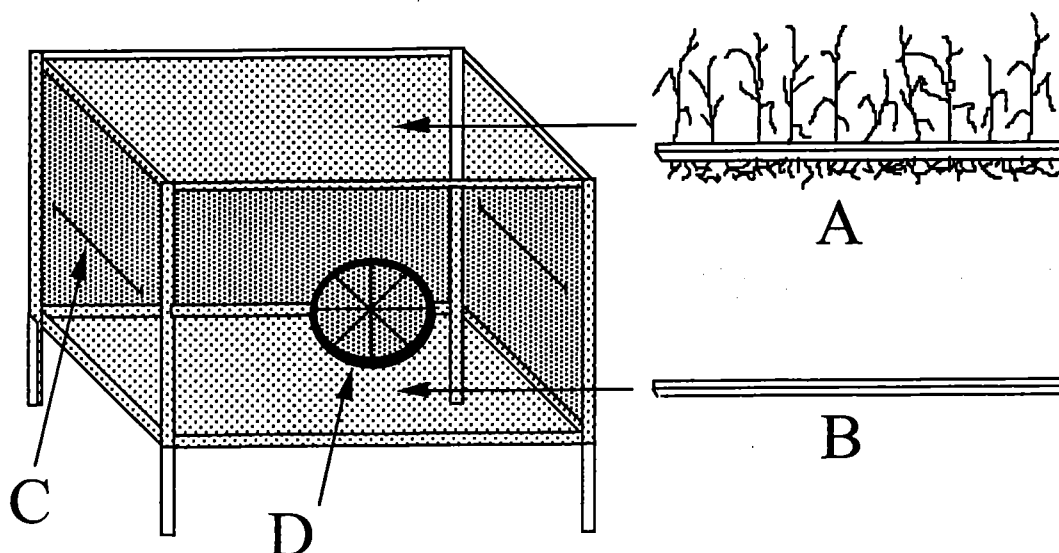


Fig. 1. Oviposition component of the spittlebug rearing unit. A tray with roots and nymphs (A), or an empty tray serve as lids. At the bottom another tray slides in with oviposition substrate (B). Stems of potted adult host plants enter through lateral slits (C) and another entrance allows manipulation inside (D).

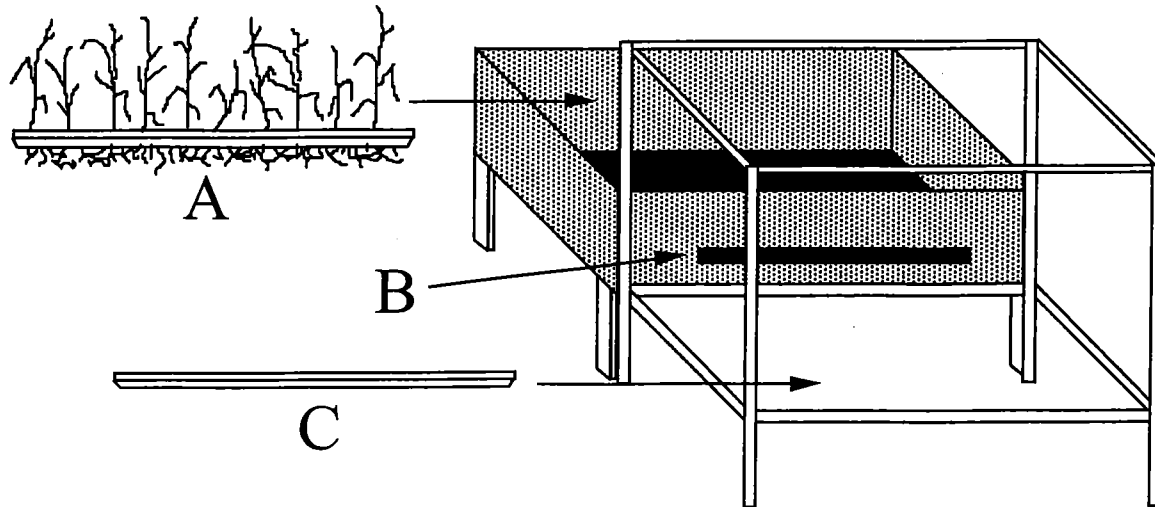


Fig. 2. Spittlebug rearing unit with nymphal rearing and adult oviposition components. The tray with roots and nymphs (A) is put on top of the wooden frame. New adults exit the frame (B) and enter the oviposition chamber (wrapped with shade cloth) with a tray of oviposition substrate (C).

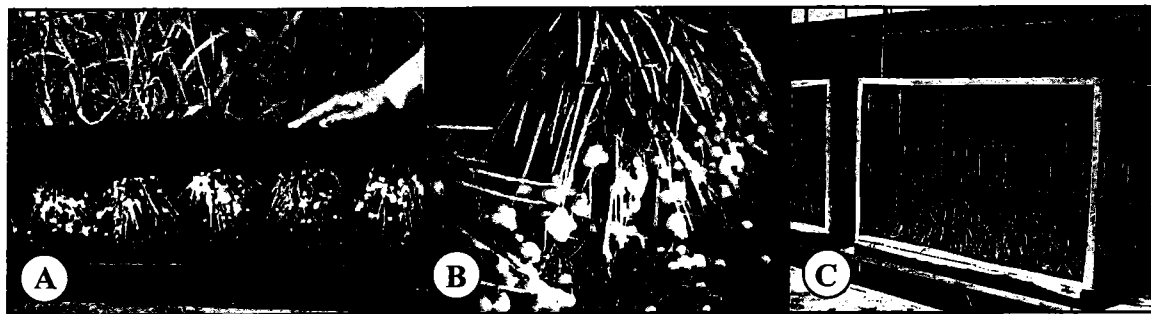


Fig. 3. Components of the mass-rearing colony, including box with host plants anchored to mounds of soil and covered with shade cloth (A), root and spittle mass development (B) and emergence cage for adult capture (C).

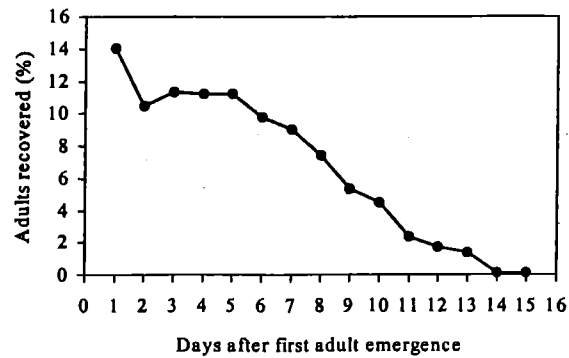


Fig. 4. Mean daily emergence rates of adult *A. varia* from mass-rearing colony. The first collection date is the sum of individuals emerged over the first 2–4 d.

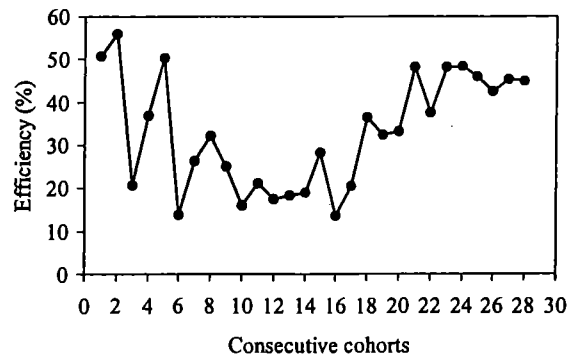


Fig. 5. Efficiency (adults from eggs) of the new mass-rearing colony for *A. varia* over 28 consecutive weekly cohorts.

FIRST RECORDS OF THE SUGAR CANE AND FORAGE GRASS PEST *PROSAPIA SIMULANS* (HOMOPTERA: CERCOPIDAE) FROM SOUTH AMERICA

sometido al:
Florida Entomologist

DANIEL PECK, ULISES CASTRO, FRANCISCO LÓPEZ, ANUAR MORALES AND JAIRO RODRÍGUEZ
Centro Internacional de Agricultura Tropical (CIAT), Apartado Aéreo 6713, Cali, Colombia

Resumen. El género *Prosapia* Fennah y *P. simulans* (Walker) son reportados por primera vez en Suramérica, basado en recolecciones recientes del campo en Colombia y especímenes de museo de Venezuela. *Prosapia simulans* fue encontrado en *Brachiaria decumbens* Stapf, *B. dictyoneura* (Fig. & De Not.) Stapf, *Cynodon plectostachyus* (K. Schum.) Pilger, y *Saccharum officinarum* L. (Poaceae). Las poblaciones detectadas en campo llegaron a niveles económicos en pastos mejorados de *B. decumbens*. En una ocasión se encontraron adultos sobre caña de azúcar. La evidencia sugiere que esta plaga centroamericana de caña de azúcar y gramíneas forrajeras es una nueva llegada, así representándose una amenaza potencial a la producción de pastos y caña en el Valle del Cauca en Colombia. Se resume la distribución, las bionómicas, y el estado de plaga de *P. simulans*, y se discute su modo de introducción y estado de plaga potencial.

GRASSLAND SPITTLBUGS (Homoptera: Cercopidae) are native xylem-feeding insects that are broadly distributed and damaging pests of graminoid crops in the Neotropics. Major hosts include sugar cane (*Saccharum officinarum* L.) and forage grasses, particularly the widely sown and highly susceptible *Brachiaria decumbens* Stapf (Valério & Nakano 1988, Lapointe et al. 1992). This diverse group of spittlebugs, which includes dozens of species from at least 11 genera, poses a major limit to productivity and persistence of the most extensive agricultural activity in the Neotropics.

The most widely distributed species in this pest complex is *Prosapia simulans* (Walker), reported in the lowland tropics from Mexico to Panama (Hamilton 1977). To our knowledge, this species and the genus *Prosapia* Fennah have never been reported in South America. Herein we report the first field detection of *P. simulans* in Colombia, and an additional record from museum specimens collected in Venezuela. Quantitative measures of field abundance were performed to make a preliminary assessment of population density and persistence. We summarize the literature on its geographic distribution, bionomics and pest status; provide a diagnosis to distinguish it from other grassland spittlebugs in northern South America; and discuss its possible mode of introduction and pest status potential.

Initial Field Detection

We discovered three populations of *P. simulans* in the Cauca Valley of Colombia in 1999-2000. All specimens were identified using characteristics of the

male genitalia and compared with type specimens at the Natural History Museum (BMNH), London.

The first report was obtained 2-VI-1999 when a single female was captured in the course of weekly surveys to document population fluctuations of the common local spittlebug species *Zulia carbonaria* (Lallemand). The site was located in a pasture of *Brachiaria dictyoneura* (Fig. & De Not.) Stapf in the Department of Cauca at 1060 m elev. (Municipio Santander de Quilichao, Finca Las Palmas, 3.050°N, 76.498°W) (Fig. 1). Additional surveys in surrounding pastures and sugar cane fields, and repeated surveys in the same site over the following year, did not recover more individuals.

On 2-VII-1999 a large population was discovered approximately 94 km northeast in a pasture of *B. decumbens* at 1155 m elev. (Dept. Cauca Valley, Municipio El Cerrito, Vereda Santa Helena, Finca El Mirador del Paraíso, 3.650°N, 76.240°W) (Fig. 1). On that visit *P. simulans* was the only spittlebug species present, with adults and nymphs in moderate to high abundance (unmeasured). Incidence of the insect in nearby cane fields has not yet been examined but a follow-up visit to the same pasture on 4 April 2000 verified a continued presence at greater abundance than the first visit, measured at 46.8 nymphs/m² ($n = 10$ 0.25m² quadrats) and 190 adults/50 sweeps ($n = 4$ series of 50 sweeps). Although economic thresholds based on quantitative yield loss data have never been established for grassland spittlebugs, these levels are considered highly damaging in Mexico. Padilla & Esquiliano (1966) designate them as "severe" (>30 nymphs/m² and >25 adults/50 sweeps) while Velasco & Sifuentes (1970) designate them one degree lower

as "high" (>46 nymphs/m² and >150 adults/50 sweeps).

Another population was identified on 1-II-2000 during a visit to a farm 33.4 km northwest of the previous site, but at 1535 m elev. (Dept. Cauca Valley, Municipio Yotoco, Vereda Cordobitas, Finca Canadá, 3.849°N, 76.466°W) (Fig. 1). *Prosapia simulans* was collected in two pastures of *B. decumbens* along with two other species, *Z. carbonaria* and *Zulia pubescens* (F.). A subsequent visit 6-IV-2000 found similar low densities measured at 2.3 adults/m² ($n = 20$ series of 50 sweeps) but adults were more widely distributed, detected in three additional pastures, one of *B. decumbens* and two of *Cynodon plectostachyus* (K. Schum.) Pilger. In addition, for the first time *P. simulans* (adults) were found feeding on sugar cane grown for panela (*S. officinarum*).

Voucher specimens from these populations of *P. simulans* are deposited in the Cornell University Insect Collection under Lot #1227.

Additional South American Record

A series of *P. simulans* was identified in the insect collection of the Centro Internacional de Agricultural Tropical (CIAT), Cali, Colombia (2 specimens) and BMNH (7 specimens). This material was all collected 30-V-1980 by Gerardo Pérez Nieto from Venezuela, Bolivar State, La Vergareña, in pasture, calculated to be near 6.783°N, 63.559°W (Fig. 1). No other South American specimens were found in the collections at Cornell University, the Universidad Nacional in Palmira (Cauca Valley) or the Universidad del Valle (Cauca Valley).

Distribution, Pest Status and Bionomics

The genus *Prosapia* comprises 14 species and ranges from Ontario, Canada to Panama (Hamilton 1977). Two new species from Costa Rica are being described (V. Thompson, Roosevelt University, personal communication). *Prosapia simulans* is widespread in the lowland tropics (Fig. 1). In Mexico it is reported in the states of Chiapas, Guerrero, Nuevo León, Oaxaca, Querétaro, San Luis Potosí, Tabasco, Tamaulipas and Vera Cruz (Fennah 1953, Clark et al. 1976, Agostini et al. 1981), within 70 miles of the United States border. We know of no published records of *P. simulans* in Texas or the southern United States although regional museum collections have not been examined. This species also occurs throughout Central America, reported from Belize, Costa Rica, Guatemala, Honduras, Nicaragua, and Panama according to Metcalf (1961) and observations (D.P.) of specimens at BMNH.

Although Guagliumi (1955) lists *P. simulans* in Colombia, the report is unsubstantiated and is probably in error.

Prosapia simulans attacks many of the major forage grass species in this geographic range. Grass hosts include *Cenchrus ciliaris* L. (Enkerlin & Morales 1979), *Cynodon nlemfuensis* Vanderyst (Peck 1999), *Digitaria decumbens* Stent (Oomen 1975), *Paspalum notatum* Fluggé (V. Thompson, personal communication), *S. officinarum* (Box 1953, Oomen 1975), and *Zea mays* L. (Ballou 1936). Four additional species are reported as acceptable hosts in greenhouse studies (Enkerlin & Schwartz 1979): *Avena sativa* L., *Pennisetum glaucum* (L.) R. Br., *Setaria italica* (L.) P. Beauv. and *Sorghum* sp. The only non-graminoid host (adults only) reported is the tree *Ilex haberi* (Aquifoliaceae) (Peck 1998a).

Enkerlin & Morales (1979) also add the following hosts (citing Flores et al. 1965 and Velasco 1968) but do specify if they are particular to *P. simulans* or the sympatric *Aeneolamia albofasciata* (Lallemand): *Chloris gayana* Kunth, *Cynodon plectostachyus* (K. Schum.) Pilger, *Cynodon dactylon* (L.) Pers., *Echinochloa polystachya* (Kunth) Hitchc., *Hyparrhenia rufa* (Nees) Stapf, *Panicum purpurascens* Raddi, *Panicum maximum* Jacquin, and *Pennisetum purpureum* Schumacher.

With the notable exception of the Cauca Valley of Colombia, essentially all cane-producing regions of Central and South America have experienced major spittlebug pest problems. The spittlebug *Aeneolamia varia* (F.) almost brought an end to the cane industry in Trinidad and other Caribbean regions at the turn of the century (Williams 1921). A diverse complex of other species have a long history with Brazilian cane fields (Guagliumi 1972). In the last decade, spittlebug pest status has increased in cane plantations of Ecuador and Central America. *Prosapia simulans* is an injurious sugar cane pest in Honduras and Nicaragua (J. Gaviria, CENGICAÑA, personal communication), although its pest status compared with the sympatric *Aeneolamia postica* (Walker) is probably inferior and merits examination. Although grassland spittlebugs are native to the Cauca Valley, habitat preferences and/or cultural practices have made them absent in cane plantations. Lack of spittlebug attack may also be explained by the absence of *A. varia* in the Cauca Valley, although this species is the major limit to production of improved forages in the extensive western Llanos of the country.

Information on the specific biology and behavior of *P. simulans* is very limited because little has been published in accessible journals and in most cases studies were carried out on a mixed species complex rather than *P. simulans* in particular.

Oomen (1975) reported two generations of *P. simulans* annually in *D. decumbens* pastures near the Gulf Coast of Mexico, with preoviposition plus the egg incubation stage requiring 33.5 d, nymphal stage 25.5 d, and total generation time 58 d. Velasco & Sifuentes (1970) reported a preoviposition period of 4 d, egg incubation of 18.7 d, nymphal stage of 22–48 d and total generation time of 58.4 d. Like all other species studied in pastures, nymphs and adults of *P. simulans* occur only during the wet season, while dormant eggs survive the dry season and hatch upon return of wet conditions. *Prosapia* lays eggs in the soil but like other spittlebug species a proportion are attached to the plant stem and litter (Pass & Reed 1965, Peck 1998b); we were unable to find published information specifically on *P. simulans* oviposition sites.

In all of the above studies, *P. simulans* is described as generally sharing pastures with another spittlebug species, such as *A. albofasciata* in northern Mexico, or *A. postica* in Honduras. There are no known published reports of it achieving outbreak status individually, indicating that although its pest status in forage grasses is substantial it may be inferior to other pest spittlebugs. The pest status of grassland cercopids in general has increased in forages of South America over the last decade. Increasingly affected areas include northern Argentina, Ecuador and the Andean hillsides, Caribbean coast, and Amazonian forest margins of Colombia.

Diagnosis

Prosapia simulans can be separated from the other 13 described world species of *Prosapia* by the following male genitalic and color pattern characters (Hamilton 1977): two short blunt teeth at tip of aedeagal shaft, preapical gonopore, subgenital plates appressed on inner margins, crown of head lighter than anterior margin of pronotum, one light-colored transverse band across pronotum and two across tegmen, head and tegminal bases red to brown, and mesopleura blotched with black.

A high degree of intraspecific color pattern variation and interspecific convergence makes it difficult to use this character for separating conspecifics of *Prosapia* and other cercopid genera. But on the geographic level, *P. simulans* can be separated from the other 19 species associated with wild and cultivated graminoids in Colombia and Ecuador (CIAT 1999) by dorsal color pattern: dark brown to black with one transverse band across the center of the pronotum and two across the tegmen (Fig. 2). As the only known member of the genus in South America, *P. simulans* is also distinguished by

the genus definition of Fennah (1949, 1953) and supporting male genitalia characters discussed by Hamilton (1977).

In Mexico and Central America, there is significant variation in the color and form of the transverse bands, ranging from yellow to pink/red to orange, broad to narrow, and distinct to completely obscured particularly in females (Clark et al. 1976, D.P., personal observation). The Colombian populations displayed a particular subset of this color and pattern variation. Of 18 males examined, all had narrow pale yellow tegminal bands with some reduction of the posterior band. The color of the venter was predominantly pink (55%), but some individuals were yellowish brown (28%) or intermediate (17%). Background tegmen color was usually brown (94%) but sometimes black (6%). Unlike *P. simulans* from Costa Rica (D.P., personal observation), males from the Colombian populations had black subgenital plates with black patches on the lateral sides of the abdominal sternites. Of 10 females examined, all had both tegminal bands greatly reduced to barely evident on a black background. Female venters were black with red (90%) to yellowish brown (10%) markings.

Mode of Introduction and Economic Considerations

Although the occurrence of *P. simulans* in Colombia and Venezuela could be attributed to low endemic populations only recently detected, we believe this is unlikely because *P. simulans* is an aposematic and economically important pest species. Furthermore, the Cauca Valley and Venezuela have been under relatively high surveillance. The CIAT forages program has been active in the Cauca Valley for the last 20 years and extensive fieldwork on grassland spittlebugs was conducted in the 1950's across Venezuela (Guagliumi 1955, 1956a, b, 1957).

Alternatively, *P. simulans* may have arrived through natural or human-mediated dispersal. We cannot offer a strong argument for either mode of invasion, but two scenarios should be considered. First, with the opening of the Darien Gap to agriculture and human disturbance, *P. simulans* may have slowly spread into northwest Colombia. Although cercopids are not known for migrations, they are capable of flights of several kilometers (Peck 1999), facilitating their dispersal to new pasture patches and forest edges. From there *P. simulans* could have spread into Colombia's Chocó region and down the Pacific coast. Unfortunately, there are no known collections of cercopids from this remote area to test this mode of introduction. It is notable, however that the Cauca Valley, is physically disjunct

from northwest Colombia by the western cordillera of the Andes.

Second, infested material may have introduced *P. simulans* from Central America if eggs were carried in associated soil and litter, or attached to plant stems. Quarantine procedures for sugar cane, at least, are highly controlled in Colombia and therefore an unlikely route of entry. It is not known how controlled the entry of forage grass material is, but international movement is usually limited to seeds. Nevertheless, it is hard to imagine the arrival of *P. simulans* to the distant site in inland Venezuelan by natural dispersal.

Broader surveys should be carried out to identify the extent of *P. simulans* populations and monitor their spread in pastures and cane plantations of the Cauca Valley. At the spittlebug densities detected in this study, milk and beef cattle production will be negatively affected and the persistence of improved *B. decumbens* pastures will be compromised. Spread or introduction of this species to lowland regions of Colombia such as the Caribbean coast or the extensive eastern Llanos could have severe economic implications. Up to now, *P. simulans* has not been reported on sugar cane beyond the single observation noted above. Nevertheless, because the evidence suggests that *P. simulans* was introduced, cane producers should consider this species a potential threat. The menace may be heightened now as management shifts from preharvest burning to green production by the year 2005; elimination of burning may increase the susceptibility of sugar cane to this new insect pest.

Finally, these observations highlight the need for care in transfer of vegetative and soil materials associated with cercopid host plants. There is some other anecdotal evidence for regional introductions of grassland spittlebugs such as *Z. carbonaria* from the Cauca Valley into the Colombian Amazon, and an isolated report of the Central Brazil species *Notozulia entreriana* (Berg) in the Colombian Llanos (Peck in prep). One well-documented case is *Lepyronia coleoptrata* (L.) (Homoptera: Aphrophoridae), a Palearctic spittlebug with immigrant status in the United States (Hoebeke & Hamilton 1983). With the increasing movement of vegetative material throughout the Caribbean Basin and northward insect range expansion due to warming trends, sugar cane and forage grass production in the southern United States, like the Cauca Valley, would be threatened by the arrival of new spittlebug pests. The southeast United States already suffers from the native *Prosapia bicincta* (Say), a damaging pest of forage grass, turf grass and ornamentals (Fagan & Kuitert 1969, Braman & Pendley 1993, Braman & Ruter 1997).

Acknowledgements

We thank V. Thompson (Roosevelt University) for alerting us to specimens of *P. simulans* from Venezuela in the CIAT collection, Gilberto Córdoba (CIAT) for finding the first large population of *P. simulans* in Colombia, and Mick Webb for access to the collection at the Natural History Museum. E. R. Hoebeke (Cornell University) and V. Thompson provided valuable comments for improving the manuscript.

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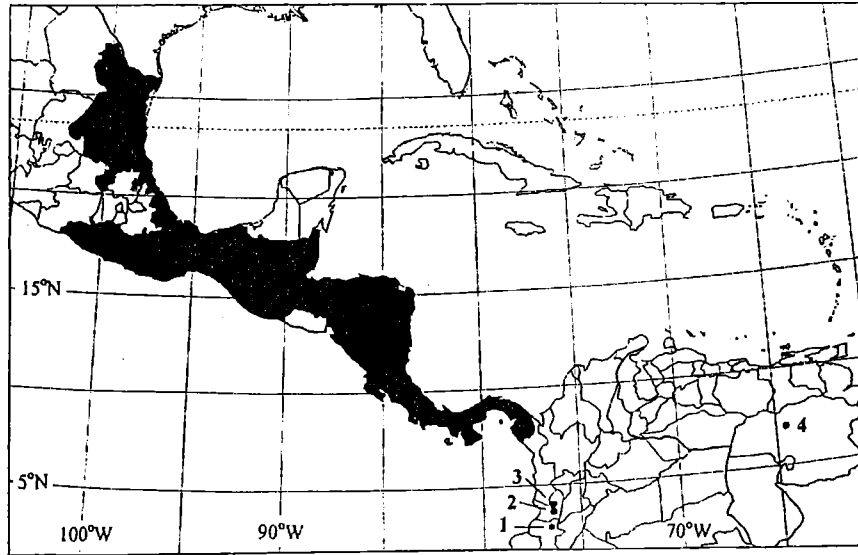


Figure 1. Known geographic distribution of *Prosapia simulans* in Mexico (by state) and Central America (by country) with new locations (by number) in South America where it was collected in Colombia and Venezuela: 1) Santander de Quilichao, Cauca 2) El Cerrito, Cauca Valley, 3) Yotoco, Cauca Valley, and 4) La Vergareña, Bolivar.

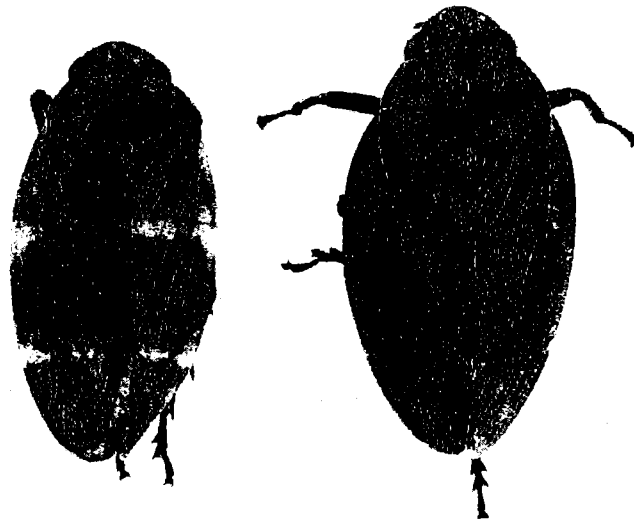


Figura 2. *Prosapia simulans* showing most common dorsal color patterns of male (left) and female from newly detected populations in Cauca Valley, Colombia.

COMUNICAÇÃO CIENTÍFICA

OCORRÊNCIA DE *Anagrus* sp. (HYMENOPTERA: MYMARIDAE) PARASITANDO OVOS DE *Deois flavopicta* (STAL) (HOMOPTERA: CERCOPIDAE) EM PASTAGENS DO BRASIL CENTRAL

Carmen S. S. Pires¹, Eliana M. G. Fontes¹, Edison R. Sujii¹, Hermínia M.C. Fernandes¹ e Dagoberto F. Gomes¹

ABSTRACT

Ocurrence of *Anagrus* sp. (Hymenoptera: Mymaridae) Parasitizing Eggs of *Deois flavopicta* (Stal) (Homoptera: Cercopidae) in Pastures of Central Brazil

Egg parasitism of *Deois flavopicta* (Stal) by *Anagrus* sp. (Hymenoptera: Mymaridae) in Distrito Federal, Brazil is recorded for the first time. After four years of field collecting diapausing eggs of the pasture spittlebug, *D. flavopicta* we found 1,66% (n = 3728 eggs) egg parasitism by *Anagrus* sp. in pastures of *Brachiaria decumbens* around Brasília. Possibilities for the use of this parasitoid as biological control agent of *D. flavopicta* is discussed.

KEY WORDS: Insecta, egg parasitoid, pasture, spittlebug.

Os adultos da cigarrinha das pastagens *Deois flavopicta* (Stal) (Homoptera: Cercopidae) sugam as folhas, e os imaturos sugam a base do colmo e as raízes expostas de gramíneas hospedeiras. Parte do ciclo de vida de *D. flavopicta* é passado no solo, onde são depositados os ovos. No Distrito Federal (DF) a cigarrinha das pastagens ocorre de novembro a maio, em três picos populacionais, não simultâneos. De maio a outubro ela fica em diapausa, na fase de ovo, em resistência à estação seca (Fontes *et al.* 1989).

Durante quatro anos, com o objetivo de estudar a influência da

Recebido em 03/07/92.

¹EMBRAPA/CENARGEN, Área de Controle Biológico, Caixa Postal 02372, 70849-970, Brasília, DF.

temperatura e da umidade sobre a diapausa da cigarrinha, foram coletados ovos diapáusicos durante a estação seca (maio a setembro), em áreas cobertas com *Brachiaria decumbens*, na região do Distrito Federal. Trazidos ao laboratório, estes ovos foram expostos à baixas temperaturas (15 - 18°C) e depois colocados à 28°C. Assim, a diapausa foi interrompida e o embrião reiniciou seu desenvolvimento. Semanalmente, os ovos foram observados para o acompanhamento da eclosão das ninfas, determinando-se a viabilidade dos ovos em cada observação. No quarto ano de repetição deste estudo, observamos a ocorrência de ovos parasitados. Estes ovos foram individualizados em tubos de vidro, tampados com algodão umedecido e mantidos à 28°C. Os primeiros parasitóides emergiram, em média, 30 dias após os ovos serem submetidos a condições favoráveis, enquanto que os ovos não parasitados demoraram em média, 15 dias para completarem o desenvolvimento. Isto demonstra o sincronismo existente entre o hospedeiro e o parasitóide. Este, como a cigarrinha, deve passar também por um período de diapausa durante a estação seca no DF. Quando as condições ambientais se tornam favoráveis, com a chegada das chuvas, os ovos não parasitados da cigarrinha saem da diapausa ocorrendo a eclosão das ninfas. Somente após um período de 15 dias, é que emergem os parasitóides adultos. Assim, quando os adultos dos parasitóides começam a emergir, a cigarrinha já completou a fase ninfal e os primeiros adultos já estão no campo realizando as primeiras posturas.

Os parasitóides foram identificados como sendo do gênero *Anagrus* da família Mymaridae, Hymenoptera. Cerca de 3728 ovos foram observados. Apenas 1,66% dos ovos estavam parasitados, com uma média de 4,53 parasitóides/ovo. *D. flavopicta* é endêmica das regiões Sul e Sudeste do Brasil, e ocorre naturalmente em capins nativos. Com a introdução de gramíneas exóticas para o pastejo, *D. flavopicta* começou a explorar estes capins, principalmente os do gênero *Brachiaria*. É possível que *Anagrus* sp. ocorra com maior frequência em ovos de *D. flavopicta* depositados nas gramíneas nativas, e que apenas recentemente tenham colonizado as pastagens introduzidas. Isto poderia explicar a baixíssima taxa de parasitismo observada no campo. O gênero *Anagrus* é citado por Huber (1986) como parasita de ovos de outras espécies de cercopídeos pragas de pastagens e de cana-de-açúcar, as espécies da família Mymaridae, geralmente parasitam ovos de inseto postos em locais oclusos, tais como dentro de tecidos de plantas, ou colocados no solo. Espécies da família Mymaridae têm sido pouco utilizadas em programas de controle biológico, apesar do potencial existente. Huber (1986) cita casos em que espécies desta família, incluindo o gênero *Anagrus*, foram deliberadamente transferidos de um país ou continente para outro, estabelecendo-se com sucesso. Outros exemplos são citados onde espécies de Mymaridae nativas foram manipuladas contra pragas também nativas. No entanto, há grande escassez de estudos básicos sobre o ciclo de vida destes insetos e de suas relações com os seus hospedeiros. A falta destes conhecimentos levou ao insucesso de muitas das tentativas de

utilização de mimarídeos em programas de controle biológico. Esse foi o caso da espécie *Acmopolynema hervali* Gomes que foi testado em 1969 em Cabo, Pernambuco, para o controle da cigarrinha *Mahanarva posticata* Stal em cana-de-açúcar (Vilas Boas & Andrade, 1990).

Anagrus sp. foi relatado como parasitóide de ovos de *D. flavopicta* por Reis & Mendes (1983) em Minas Gerais, porém nenhum registro na literatura foi feito até o momento para a região do Distrito Federal. O potencial de *Anagrus* sp. como agente de controle biológico de *D. flavopicta* nas pastagens do Brasil Central poderá ser determinado após estudos sobre percentagem de parasitismo durante a estação chuvosa, ciclo biológico, flutuação populacional e comportamento do parasitóide em pastagens nativas e introduzidas.

AGRADECIMENTOS

Ao Dr. Paul Hanson, Escuela de Biologia, Universidad de Costa Rica e ao Dr. Fred Bennett, University of Florida, EUA, pela identificação do material.

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Preference–performance linkage in the neotropical spittlebug *Deois flavopicta*, and its relation to the Phylogenetic Constraints Hypothesis

C. S. S. PIRES,¹ P. W. PRICE² and E. G. FONTES¹ ¹Embrapa Recursos Genéticos e Biotecnologia, Brazil and ²Northern Arizona University, Flagstaff, Arizona, U.S.A.

Abstract. 1. Predictions from the Phylogenetic Constraints Hypothesis were tested for the first time in a tropical system using the pasture pest *Deois flavopicta* Stål, which oviposits into the ground and not into plant tissues. The prediction that there is no oviposition preference–larval performance linkage was supported. The absence of such a link provides an evolutionary basis for eruptive population dynamics.

2. The effects of host species and host plant quality on the preference of ovipositing females of *D. flavopicta* and performance of their offspring on the selected host plants were tested at the population level.

3. Female oviposition behaviour was affected by the presence of the host plant. Females of *D. flavopicta* showed a strong preference to oviposit close to host plants. The number of eggs was higher in pots containing *Brachiaria ruziziensis* (121.88 ± 13.70) than in pots containing only the wet oviposition substrate (5.2 ± 1.98) or dry oviposition substrate (0.067 ± 0.067). Ovipositing females did not, however, discriminate between plants of *Brachiaria decumbens* and *Axonopus marginatus* and did not show a strong oviposition preference in relation to differences in plant quality (protein and fibre content). They did show oviposition preference for plants under the high watering regime. The mean number of eggs collected from pots with non water-stressed plants was 60% higher than the mean number of eggs collected on pots with water-stressed plants.

4. Although females did not show ovipositional preference, spittlebug larval performance, measured as percentage survival and duration of nymphal period, was better on plants of high protein and low fibre content. These results indicate that there is not a linkage between female oviposition preference and subsequent nymphal performance in relation to differences in protein and fibre content in the host plants. There was, however, a limited linkage between oviposition preference and nymphal performance in relation to plant water content. Females showed preference for moist sites that have high survival of newly hatched nymphs.

5. Evidence indicates that for *D. flavopicta*, the influences of natality and female oviposition behaviour in response to plant quality are not the major factors driving population outbreaks, which is in accordance with the Phylogenetic Constraints Hypothesis.

Key words. Insect outbreaks, nymphal performance, ovipositional preference, population dynamics.

Introduction

Patterns in population dynamics among insect species have been detected in nature, and hypotheses to explain these patterns have been proposed, but few studies have searched for

Correspondence: Carmen Pires, Embrapa Recursos Genéticos e Biotecnologia, Cx. Postal 02372, Brasília, DF, 70.849-970, Brazil. E-mail: cpires@cenargen.embrapa.br

broad and repeatable patterns and in most cases the mechanistic explanations for these patterns have been tested poorly (Tilman, 1989; Price, 1991; Price *et al.*, 1995a).

A new approach to population dynamics studies, which emphasises the importance of a linkage between oviposition preference and offspring performance on the population dynamics of herbivorous insects, has been proposed (Price *et al.*, 1990, 1995a; Price, 1994). Based on studies of different latent species of gall-forming sawflies of the genus *Euura* and on the life-history traits and patterns of population dynamics described in the literature for a very wide range of herbivorous insects, Price *et al.* (1990) developed the Phylogenetic Constraints Hypothesis. This hypothesis argues that evolved life-history characteristics, such as female choice of oviposition sites, have direct consequences for the pattern of the plant-herbivore interaction and the population dynamics of herbivorous insects (Price *et al.*, 1995a).

According to the Phylogenetic Constraints Hypothesis, the fundamental difference between latent and eruptive species is that females of latent species can evaluate plant quality as a resource for larvae, while females of eruptive species cannot (Price, 1994). The hypothesis predicts that for latent species a strong linkage between preference and performance has evolved (Price *et al.*, 1990, 1995a; Price, 1994). The females of latent species oviposit preferentially on high quality resources where larvae must establish and usually exhibit higher survival rates. These high quality sites are rare in the plant population, so competition among females for oviposition sites can be high, however females can disperse relatively long distances in search of resources when these are locally limiting. The spacing of eggs by females prevents larval competition so that resources will not be overexploited and the host plant will not be killed. Thus these species are less likely to become serious pests.

For eruptive species, however, the hypothesis predicts a weak linkage between oviposition site selection and offspring performance (Price *et al.*, 1990, 1995a; Price, 1994). As a consequence of female oviposition behaviour, larvae of eruptive species feed away from the oviposition site and tend to be more generalised in resource utilisation. The resource is often abundant and there is no competition for oviposition sites among females. Consequently there is no emigration of females from dense populations, resulting in high densities of larvae. Because the larvae are generalists and feed on most parts of the host plant, the plants can be killed. In these species, the nonspecific oviposition behaviour of females and the generalised feeding behaviour of larvae can allow populations to reach high densities.

The observed relationships between oviposition preference and various components of offspring performance range from good to poor correspondence [see Thompson (1988) and Thompson & Pellmyr (1991) for a review]. Linkage between preference and performance has been recorded repeatedly in natural populations of different species of sawflies of the genus *Euura* (Price *et al.*, 1987; Price, 1989; Roininen *et al.*, 1993; Woods *et al.*, 1996) and tested experimentally in *Euura lasiolepis* Smith (Price & Clancy, 1986; Preszler & Price, 1988; Craig *et al.*, 1989) and in the nymphalid butterfly

Euphydryas editha Bdv. (Singer, 1983; Singer *et al.*, 1988). All results are consistent with the Phylogenetic Constraints Hypothesis.

Three studies have tested the preference-performance linkage in eruptive species (Legg *et al.*, 1986; Dodge & Price, 1991; Leyva, 1996). No evidence of a linkage between oviposition preference and offspring performance was found for the European corn borer *Ostrinia nubilalis* Hübner (Legg *et al.*, 1986), the chrysomelid beetle *Disonycha pluriligata* LeConte (Dodge & Price, 1991), or the western spruce budworm *Choristoneura occidentalis* Freeman (Leyva, 1996). For a broader general hypothesis to be developed, however, it needs to be tested in other insect groups, and it is important to test hypotheses in tropical systems.

The spittlebug-grass system offers an opportunity to test the preference-performance linkage in conditions very different from those in which the hypothesis was generated and tested previously. The spittlebug *Deois flavopicta* Stål (Homoptera: Cercopidae) and *Euura* species have very different life histories (Fontes *et al.*, 1995; Price *et al.*, 1995a). *Deois flavopicta* is a free-feeding herbivore that feeds on sap of different species of grasses, while species in the genus *Euura* are all plant gallers on shrubs and trees. Unlike the *Euura* species, spittlebug females do not oviposit in the plant tissue. Females of *D. flavopicta* lay eggs in the soil around the base of host plants. Ovipositing away from the host plant is apparently an old trait in the grass-feeding spittlebug group (Table 1). Different species of the genus *Deois* and several species of the different cercopid genera show this oviposition behaviour and all are eruptive species on different grass species.

For *D. flavopicta*, therefore, a low or no preference-performance linkage between oviposition site selection and nymphal performance is predicted. In order to test this prediction, the effects of host plant species and differences in host plant quality on oviposition preference and offspring performance in *D. flavopicta* were examined and the following questions were addressed: (1) Is the oviposition behaviour of the herbivore affected by the presence of the host plant? (2) If so, is there an oviposition preference in relation to the different host species and host plant quality? (3) How do plant species and plant quality affect offspring performance? (4) Is there a linkage between oviposition preference and nymphal performance?

Methods

The insect

The spittlebug *D. flavopicta* is a neotropical species, with a natural distribution throughout the South-East and Central-West regions of Brazil. This species fed originally on native grasses and exhibits low population density on cerrado, the Brazilian savanna (Pires, 1998). With the introduction of exotic grasses, principally species of the genus *Brachiaria* from Africa, *D. flavopicta* populations rose to high levels and outbreak on pasture cultivated with the introduced grass species (Fontes *et al.*, 1995). *Deois flavopicta* is currently the

ominant pasture pest species in the Central-West region of Brazil.

In the Federal District of Brazil (Brasília) (15°31'–16°03'S, 7°21'–48°15'W), where this study was conducted, *D. flavopicta* has three population peaks of adults during the rainy season, from October to May, and diapauses in the egg stage during the dry season (Fontes *et al.*, 1995). The size and timing of *D. flavopicta* population peaks vary from year to year in relation to the annual rainy season (Fontes *et al.*, 1995). Adults generally emerge in November, January, and March. Diapausing eggs laid by females of the second and third generations have diapause programmed for different durations, on average 8 and 5 months, respectively. Eggs are laid in the soil close to the host plants. Nymphs feed gregariously on roots and ramets, close to the soil surface. They excrete *spittle*, a creamy liquid formed by the introduction of air bubbles into the watery excretion, and feed within the spittle mass. Both nymphs and adults suck on the sap and debilitate the plant. Adults generally feed on leaves, frequently killing them, probably by the injection of salivary secretions that cause cytotoxic effects.

Table 1. Examples of species of cercopids on the American continent.*

Species	Host plants	Oviposition site
Genus: <i>Aeneolamia</i>		
<i>varia posticata</i>	Grasses	Soil
<i>v. saccharina</i>	Sugar cane	Soil and plant debris
<i>occidentalis</i>	Sugar cane, grasses	Soil
<i>selecta selecta</i>	Sugar cane, grasses	Soil
<i>s. transversa</i>	Grasses	Soil
<i>reducta montana</i>	Grasses	Soil
Genus: <i>Deois</i>		
<i>flavopicta</i>	Grasses	Soil and plant debris
<i>incompleta</i>	Grasses	Soil and plant debris
<i>schach</i>	Grasses	Soil and plant debris
Genus: <i>Mahanarva</i>		
<i>fimbriolata</i>	Sugar cane, grasses	Dead leaf sheath and soil
<i>rubicunda indentata</i>	Sugar cane, grasses	Dead leaf sheath and soil
Genus: <i>Prosapia</i>		
<i>bicincta bicincta</i>	Grasses, legume	Soil
<i>simulans</i>	Grasses	Soil
Genus: <i>Zulia</i>		
<i>entreriana</i>	Grasses	Soil
<i>comlobiana</i>	Grasses	Soil
Other species		
<i>Hilaenus spumarius</i>	Legume	Grass stubble

*Modified from Calderín *et al.* (1982).

The host plants

The native grass *Axonopus marginatus* (Trin.) and two introduced grass species of the genus *Brachiaria*, *B. decumbens* (Stapf) and *B. ruziziensis* (Stapf), were selected for this study. Densities of nymphs on natural grasslands and on pasture were used as a guide to select the host plants utilised in the experiments (Pires, 1998). *Axonopus marginatus* is a perennial, tall-growing grass with a tussock habit and very narrow leaves (Klink, 1994). *Brachiaria decumbens* is a perennial grass characterised by a decumbent, stoloniferous growth habit, rooting from the lower nodes (Klink, 1994), and *B. ruziziensis* is a perennial grass with prostrate growth that forms swards (Ferrulino & Lapointe, 1989). Clones of the three grass species used in the experiments were collected from adjacent areas in the field and propagated vegetatively in pots.

Preference–performance evaluation

The terms *preference* and *performance* follow the definitions of Singer (1986) and Thompson (1988). Preference is a nonrandom oviposition close to the plant resource offered simultaneously in a multiple-choice cage. Performance is some measure of offspring survival, growth, or reproduction. The first experiment tested the influence of the host plant and the ovipositional substrate on ovipositional behaviour. The other three experiments investigated the linkage between ovipositional preference and nymphal performance in relation to the different host species and differences in plant quality. These experiments consisted of two parts: (1) a multiple-choice test for ovipositional preference and (2) nymphal performance on the plants chosen by females.

The multiple-choice arenas were enclosed by bottomless cages made of a metal frame with a 1.0-m base diameter, a 0.40-m top diameter, 0.70 m tall and covered with an organandy screen. In all experiments, the different treatments (potted plants) were assigned randomly to positions within cages. In expts 2 and 3, the potted plants were buried until the soil surface of the pots was level with the ground.

In all experiments, following a methodology modified from McWilliams and Cook (1975) and Kalvelage and Buzzi (1986), the soil surface of the pots was covered with a piece of paper towel over a layer of cotton to serve as the oviposition substrate. With this procedure, it was possible to standardise the humidity and texture of the oviposition substrate between replicates, and the collection of eggs was facilitated. This substrate was kept wet in all treatments in expts 2, 3, and 4.

Experiments 2 and 3 on oviposition preference were conducted in the field. The other two oviposition preference experiments and all the performance evaluation experiments were conducted in a greenhouse, where irrigation of the host plant and the humidity of the oviposition substrate were controlled. Predation on eggs and nymphs was prevented in the performance evaluation experiments. To simulate natural conditions, the greenhouse daily temperature was kept between 33.3 ± 1.2 and 16.9 ± 2.1 °C, with approximately 70% air humidity, and natural photoperiod (12–13 h of light).

In all experiments, the adults were collected randomly in pastures cultivated with *Brachiaria* no further than 5 m from a natural grassland. The sex of individual insects was determined in the laboratory, and they were released into experimental cages. Oviposition preference was evaluated at the population level, i.e. the number of eggs laid by groups of females was counted. *Brachiaria* spp. meadows were the only source of abundant insects, so there was a potential bias in preference studies resulting from females conditioned to these host plant species. The results do not, however, indicate such an effect.

Oviposition preference

Experiment 1. Three choices of sites for oviposition were offered to the females: a pot with the soil surface covered by completely dry cotton and paper towel, a pot with the soil surface covered by wet cotton and paper towel, and a pot planted with the host grass *B. ruziziensis* with the soil surface covered by wet cotton and paper towel. Fifteen males and 15 females were placed in each of the 15 replicated cages and kept in the cages for 4 days.

Experiment 2. Spittlebug oviposition preference was measured between two grass species: *A. marginatus* and *B. decumbens*. Females were offered both host plants in 20 replicated cages. A total of 25 males and 25 females was released in each cage. Fifteen pairs were released initially and kept in the cages for 5 days. The oviposition substrate and the remaining live adults were then removed, the oviposition substrate was replaced, and 10 more pairs were released in all repetitions and kept in the cages for 5 days. The number of eggs laid in each replicate by the 25 females was recorded.

Experiment 3. This experiment measured the effects of host plant quality, in terms of total protein and fibre content, on the oviposition preference and performance of *D. flavopicta*. Plants of *A. marginatus* and *B. decumbens* with and without fertilisation were offered to the females in a multiple-choice cage, totalling four different choices for oviposition in each replicate, with a total of 40 replicates. A total of 25 pairs were released in each cage. Fifteen pairs were released initially and kept in the cages for 5 days, after which the ovipositional substrate and remaining live adults were removed. The ovipositional substrate was replaced and 10 more pairs were released in all repetitions and kept in the cages for 5 days. The number of eggs laid in each replicate by the 25 females was recorded.

The plants were fertilised with the equivalent of 50 kg ha⁻¹ Ouro Verde (20–15–15 N–P–K) fertiliser 1 week before the beginning of the preference test, and three times during evaluation of nymphal performance. Plants were irrigated three times a week until soil saturation. Given 7 days for the plants to respond to the treatment, samples of leaves and stems were taken from plants of the four treatments and analysed for protein and fibre content. Samples of leaves and stems were taken from plants again 60 days after the beginning of fertilisation and analysed for fibre content. The analysis of

total protein and fibre contents was performed according to the techniques of de Oliveira (1981) and Goering and Van Soest (1970), respectively.

Experiment 4. This experiment measured the effects of water supply on host plant growth and oviposition preference and performance of *D. flavopicta*. Plants of *B. ruziziensis* submitted to high and low watering regimes were offered to the females in multiple-choice cages. Fifteen male–female pairs were released in each of 15 replicated cages and kept there for 4 days.

The high- and low-water treatments were watered twice and once a week, respectively. The watering regime began 3 weeks before the beginning of the preference test and was extended to the same interval during performance evaluation. Plants received 250 ml of water at each irrigation. After 3 weeks of the watering regime, samples of leaves and stems were taken from plants of the two treatments and analysed for water content. After 6 weeks of treatment, during the nymphal performance evaluation, 15 plants each of the high and low watering treatments were taken and the number of stems per plant was counted. The length of 10 stems taken randomly from each plant was also measured.

Data analysis. The oviposition preference for a combination of host plant and different oviposition substrates (expt 1) and for plants growing under different fertiliser regimes (expt 3) was tested using Friedman's test, a nonparametric rank procedure for testing the equality of treatment means in randomised block designs. When a significant difference was found among treatments, the Student–Newman–Keuls test, a multiple testing procedure, was used. The oviposition preference for different host species (expt 2) and for plants growing under different watering regimes (expt 4) was tested using a paired *t*-test. Each cage was used as a replicate. In all tests, the null hypothesis was rejected if $P < 0.05$.

Differences in host plant quality in relation to fertilisation were tested with ANOVA followed by Student–Newman–Keuls multiple comparison test. The responses of host plants to different water regimes were tested with one-way ANOVA and *t*-test.

Performance evaluation

The relationship between adult female size and fecundity was measured. If female size were a good predictor of fecundity, it could be used as a measure of offspring performance. A pair of male and female spittlebugs was caged on potted *B. ruziziensis* within 24 h after female emergence. The cages were checked daily until the death of each female and the number of eggs was counted. The relationship between the number of eggs laid and the length of female wings was tested using correlation analysis (Pearson Product Moment Correlation).

The progeny from the preference tests were collected as eggs from treatments of expts 2, 3, and 4, and incubated in growth chambers. For expts 2 and 3, recently emerged nymphs

were transferred to the base of host plants that had been submitted to the same conditions as the plants from which the eggs were collected. In expt 4, fully developed eggs were placed on moist paper under a layer of cotton at the base of plants treated with low or high water regimes. This procedure allowed the nymphs to hatch. Three days after infestation, the empty egg chorions were removed and plants were examined for the presence of a spittle mass. With this procedure, the effect of the water regime on the capacity for feeding initiation by newly hatched nymphs could be evaluated. Nymphs of all experiments were examined periodically until the final moult to determine the length of the nymphal stage and survival. Adults were collected, their sexes determined, then stored in a freezer for later measurement of wing length.

Data analysis. The survivorship of spittlebug nymphs was analysed for dependence on host species and host quality with chi-squared test. Average length of nymphal stage and length of female wing were analysed by Tukey's multiple comparison test, when a significant *F*-value was evident.

Results

Oviposition preference

Influence of host plant presence. Host plant and substrate moisture influenced the oviposition behaviour of *D. flavopicta*. The order of oviposition preference was: host plant + wet oviposition substrate > wet oviposition substrate without host

plant > dry oviposition substrate without plant (Friedman's test, $\chi^2 = 27.85$, d.f. = 2, $P < 0.001$; Fig. 1).

Influence of host plant quality. The fertilisation and water treatments altered host plant quality. The response to fertilisation differed between the two grass species in relation to protein content. Plants of *B. decumbens* responded to fertilisation with greater protein increases than did plants of *A. marginatus* (Table 2). Total protein contents did not differ

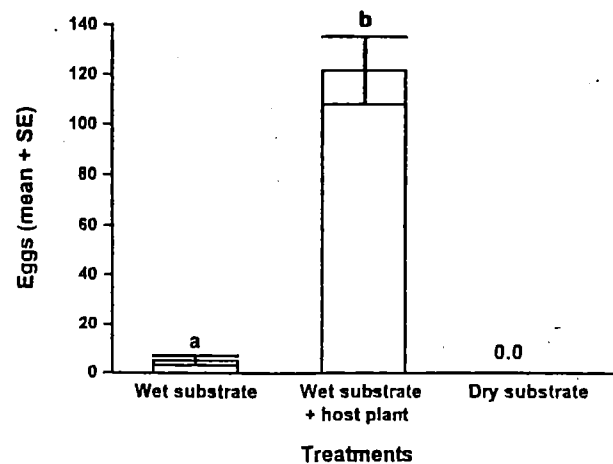


Fig. 1. Oviposition site preference of *Deois flavopicta* females. The treatments were offered in multiple-choice cages. Different letters above the columns indicate a significant difference between means (Student-Newman-Keuls, $n = 15$, $P < 0.05$).

Table 2. Total protein and fibre content in leaves and ramets of plants of *Brachiaria decumbens* and *Axonopus marginatus* with and without nitrogen, phosphorous, and potassium treatment.

	Total protein content* (7 days after treatment)	Fibre content† (7 days after treatment)	Fibre content† (60 days after treatment)
<i>decumbens</i>	7.20 ± 0.65 a‡	64.65 ± 0.06 b	62.69 ± 1.54 a
<i>decumbens</i> + NPK	15.27 ± 0.57 b	62.37 ± 0.20 c	63.64 ± 1.27 a
<i>marginatus</i>	8.47 ± 0.46 a	77.82 ± 0.21 a	69.94 ± 0.70 b
<i>marginatus</i> + NPK	10.89 ± 0.01 c	77.97 ± 0.38 a	70.11 ± 0.24 b

Values of protein content expressed as total protein (g) in 100 g of dry weight.

Values of total neutral detergent fibre (pectin, cellulose, lignin, and nonsoluble nitrogen in acid detergent) expressed as per cent of dry weight. Means followed by the same letter do not differ ($P < 0.05$, d.f. = 2, Student-Newman-Keuls multiple comparison test).

Table 3. Effect of two water regimes on plants of *Brachiaria ruziziensis*.

	Plant growth		Plant water content (% of dry weight)* (mean ± SE)
	Number of shoots (mean ± SE)	Shoot length (cm) (mean ± SE)	
High water	31.21 ± 2.87 a	15.86 ± 1.22 a	268.48 ± 4.46 a
Low water	23.15 ± 1.13 b	11.22 ± 0.85 b	243.28 ± 4.83 b
	$P = 0.015$	$P = 0.005$	$P = 0.011$

Plant water content (PWC) was recorded on a dry weight basis [$PWC = 100 \times [(fresh\ weight - dry\ weight)/dry\ weight]$].

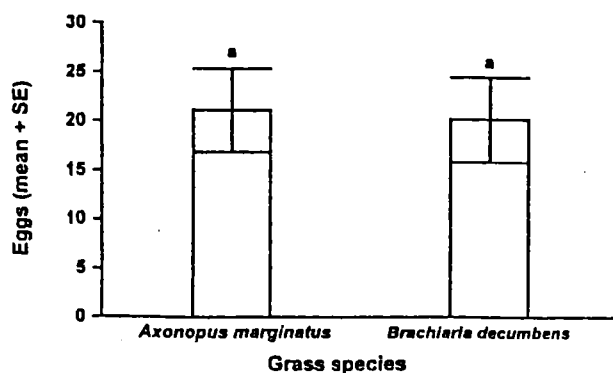


Fig. 2. Oviposition site preference of *Deois flavopicta* females when two grass species were offered in the same multiple-choice cage. Same letters above the columns indicate no significant difference between means ($t=0.177$, d.f. = 19, $n=20$, $P=NS$).

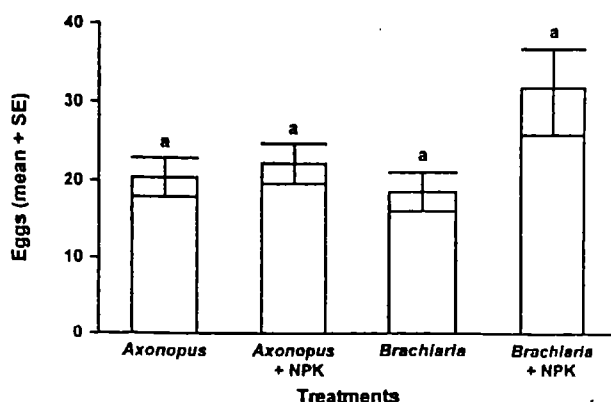


Fig. 3. Oviposition site preference of *Deois flavopicta* females when two grass species subjected to different nitrogen, phosphorous and potassium levels were offered in the same multiple-choice cage. Same letters above the columns indicate no significant difference between means (Friedman's test, $\chi^2=7.144$, d.f. = 3, $n=40$, $P=NS$).

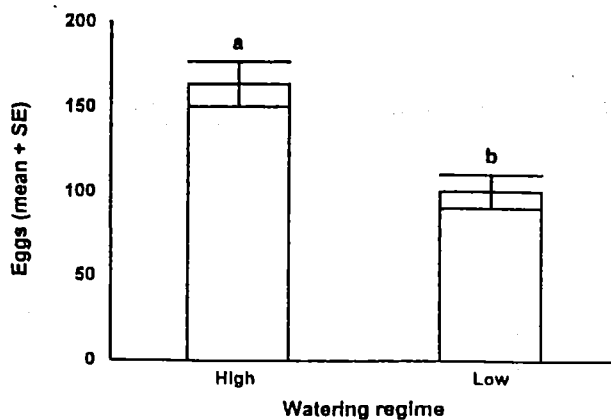


Fig. 4. Oviposition site preference of *Deois flavopicta* females when plants of *Brachiaria ruziziensis* subjected to different watering regimes were offered in the same multiple-choice cage. Different letters above the columns indicate a significant difference between means ($t=3.936$, d.f. = 28, $n=29$, $P<0.001$).

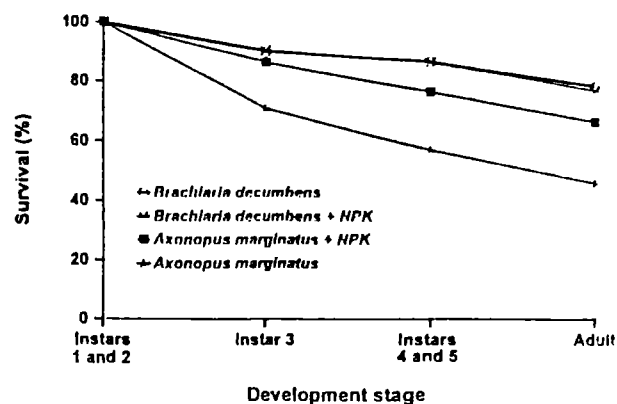


Fig. 5. Survivorship of nymphs of *Deois flavopicta* reared on two grass species subjected to different nitrogen, phosphorous and potassium levels. Cohorts started with nymphs that initiated feeding on plants: *B. decumbens*, $n=198$; *B. decumbens* + NPK, $n=361$; *A. marginatus*, $n=317$; *A. marginatus* + NPK, $n=414$ ($\chi^2=92.02$, d.f. = 3, $P<0.001$).

significantly between nonfertilised plants of both species, but fibre content on nonfertilised *B. decumbens* plants was lower than on nonfertilised *A. marginatus* plants (Table 2). Fertilisation did not alter the fibre content of either grass species. Plant water content was significantly higher in plants of the high water treatment ($t=3.64$, d.f. = 6, $P<0.05$; Table 3). The mean number of shoots was significantly higher in the high-water treatment than in the low-water treatment ($t=2.61$, d.f. = 26, $P<0.05$; Table 3), and shoots were significantly longer in the high-water treatment than in the low-water treatment ($t=3.08$, d.f. = 25, $P<0.01$; Table 3).

Despite the differences in plant quality, females did not show strong oviposition preference in relation to differences in plant species and plant quality. Females did not show oviposition preference when their native and introduced host plants were offered in multiple-choice cages ($t=0.177$, d.f. = 19, $n=40$, $P=NS$; Fig. 2). Oviposition preference did not differ significantly in relation to host plant fertilisation, despite the fact that the mean number of eggs laid on fertilised plants of *Brachiaria* was higher than the mean number laid on the other treatments (Friedman's test, $\chi^2=7.144$, d.f. = 3, $n=40$, $P>0.05$; Fig. 3). Spittlebug females, however, showed ovipositional preference for plants under the high watering regime ($t=3.936$, d.f. = 28, $n=29$, $P<0.001$; Fig. 4). The mean number of eggs collected from pots with non water-stressed plants was 60% higher than the mean number of eggs collected on pots with water-stressed plants.

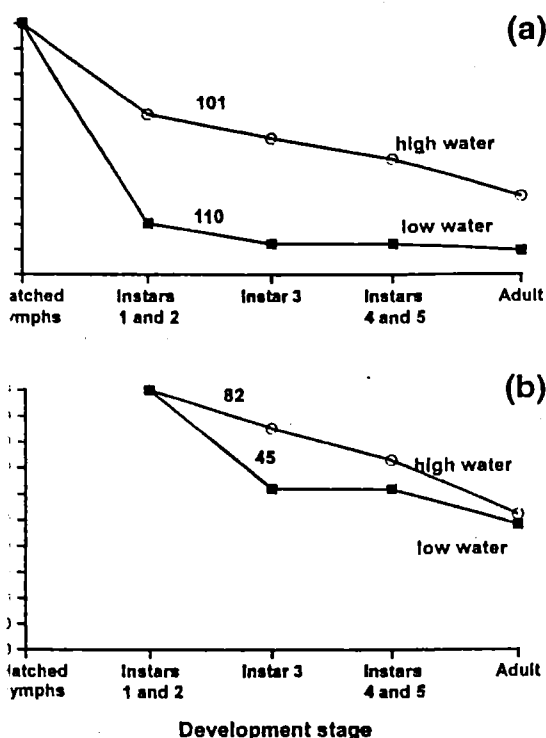
Nymphal performance

Fecundity was not correlated significantly with female wing length ($r^2=0.054$, $n=93$, $P=NS$). Because projections of future fecundity based on female size would be very imprecise, female wing size was not used as a measure of performance. Females reared on *B. decumbens* (with and without nitrogen, phosphorous, and potassium), however, were significantly

Nymphal developmental time and wing length of females obtained from nymphs of *Deois flavopicta* reared on two grass species with or without fertiliser treatment.

	Developmental time (days) *		Female wing length (cm) †	
	n	Mean ± SE	n	Mean ± SE
<i>Decumbens</i> + NPK	156	44.15 ± 0.49 ab	125	0.82 ± 0.004 a
<i>Decumbens</i>	116	42.61 ± 0.52 a	60	0.82 ± 0.006 a
<i>Marginatus</i> + NPK	233	43.28 ± 0.41 a	87	0.79 ± 0.004 b
<i>Marginatus</i>	136	46.58 ± 0.58 b	47	0.78 ± 0.006 b

each column followed by the same letter do not differ: * $P > 0.05$, Tukey multiple comparison test, † $P > 0.05$, Dunn's multiple comparison test.



Survivorship of nymphs of *Deois flavopicta* reared on *A. marginatus* plants subjected to different watering regimes. (a) Cohorts started with newly hatched nymphs ($\chi^2 = 23.80$, d.f. = 1, $P < 0.001$). (b) Cohorts started with nymphs that initiated feeding on the plants ($\chi^2 = 5.35$, d.f. = 1, $P = \text{NS}$). Initial number of nymphs is shown above each curve.

on those reared on plants of *A. marginatus* (with and without nitrogen, phosphorous, and potassium) (Table 4). Nymphal survival and length of nymphal cycle were therefore used as measures of nymphal performance.

There was a significant difference in nymphal performance between the two grass species (Table 4, Fig. 5). Survivorship on introduced grass, *B. decumbens*, was higher (77.78%) than on the native grass, *A. marginatus* (45.74%) (Fig. 5). Plant fertilisation produced different effects on nymphal performance on the two grass species. Nymphal survivorship was higher on fertilised plants of *A. marginatus* (65.94%), but

plant fertilisation did not produce a difference in nymphal survivorship on plants of *B. decumbens*. Nymphal survivorship on *B. decumbens* with nitrogen, phosphorous, and potassium (76.40%) was very similar to survivorship on nonfertilised plants of the same species (77.78%). When the total survivorship on nonfertilised plants and fertilised plants of both species was compared, this survivorship pattern was significantly nonrandom ($\chi^2 = 92.02$, d.f. = 3, $P < 0.001$; Fig. 5). Fertilisation also increased the nymphal cycle on plants of *B. decumbens* (Table 4).

The nymphal performance also differed between plants of *Brachiaria* submitted to the low and high water regime. Total survivorship to adult stage, measured when the cohorts started with newly hatched nymphs, was higher on plants on the high water regime (Fig. 6a). This survivorship pattern was significantly nonrandom ($\chi^2 = 23.80$, d.f. = 1, $P < 0.001$; Fig. 6a). When the cohort started with nymphs that had already initiated feeding on the plants, however, no difference was observed between survival of nymphs reared on plants submitted to low- and high-water treatments ($\chi^2 = 5.35$, d.f. = 1, $P > 0.05$; Fig. 6b). These results indicate that water stress on plants caused higher mortality of newly hatched nymphs. In addition, duration of nymphal development was significantly shorter on non water-stressed plants (44.33 ± 1.66 days) than on water-stressed plants (56.79 ± 3.41 days) ($t = -3.863$, d.f. = 57, $P < 0.001$).

In summary, the results indicated that there is no evidence to support a strong linkage between female oviposition preference and subsequent nymphal performance. Spittlebug nymphs performed better when reared on plants with high nitrogen and low fibre content. Nevertheless, females did not show preference for ovipositional sites in relation to differences in host species and host-plant quality (protein and fibre contents). There was, however, a positive linkage between oviposition preference and nymphal performance, measured as survival of newly hatched nymphs, in relation to water plant content.

Discussion

The prediction of the Phylogenetic Constraints Hypothesis for eruptive species, that there is no link between oviposition

preference and larval performance, was supported in part for *D. flavopicta*. Results presented here show limited linkage between oviposition site selection and nymphal performance in *D. flavopicta*, primarily for young larval survival in relation to water content in the host plants. In this species, the female oviposition behaviour of laying eggs in the soil, the free-feeding habit of the nymphs, and the long diapause of eggs reduce the probability of a strong preference-performance linkage evolving. Due to female oviposition behaviour, the newly hatched nymphs must forage for themselves. *Denis flavopicta* larvae must forage on the ground and initiate feeding on the ramet nearest their hatching site, without showing a strong preference among ramets based on plant quality or module size. In this situation, larvae must evolve the capability to utilise all or most ramet qualities to survive, and the population can increase and cause substantial damage on the host plants. Previous results showed a haphazard host-plant selection by third- and fourth-instar nymphs in relation to the ramet size of their host plant *B. ruziziensis* (Price *et al.*, 1995b). According to Thompson (1988), for insect species that can move often between plants during development, preferences for plant species can be expressed in both adults and immatures, unlike insects that finish development on a single plant. Hence, there is a potential for selection on preference to act differently in adults and immatures (Wiklund, 1975; Thompson, 1988). In addition, because of the long diapause of eggs, 8 months and 5 months on average for eggs laid during the second and third generations, respectively (Fontes *et al.*, 1995), females of *D. flavopicta* are unable to assess the quality of the food on which their offspring will feed, so the potential for selection to act on oviposition site preference is low.

Females of *D. flavopicta* showed a strong preference to oviposit in the substrate close to their host plants. These results are consistent with previous studies showing that a higher egg density is found in soils and plant debris close to the host plant, *B. decumbens*, than in open areas between grass clumps (Nilakhe *et al.*, 1984; Hewitt, 1986). Hewitt (1985) showed that females also preferred to oviposit in moist, compact soils composed of small particles. In the study reported here, ovipositing females did not discriminate between plant species and did not show an ovipositional preference in relation to differences in plant quality (nitrogen and fibre contents), but they did show an oviposition preference for wet soil. The lack of oviposition preference in relation to different host species is in accordance with other research conducted with grass-feeding spittlebugs. Although Hewitt (1986) found more spittlebug eggs in pasture cultivated with *B. decumbens* than in pastures cultivated with two other *Brachiaria* species, experimental studies did not find strong ovipositional preference in relation to different host plants (Nilakhe, 1987; Cosenza *et al.*, 1989). Nilakhe (1987) and Cosenza *et al.* (1989), working with *Zulia entreriana* (Homoptera: Cercopidae) and *D. flavopicta*, respectively, did not find a strong oviposition preference in relation to different introduced host plants offered in a multiple-choice cage. Overall, these studies support the results presented here, indicating that differences in host plant quality may not be an important factor in a female's choice of oviposition sites.

Although females did not show a strong ovipositional preference, nymphal performance, measured as percentage of survival and duration of nymphal period, was superior on plants with high protein and water contents, and low fibre contents. The lower percentage of fibre in plants of *B. decumbens*, compared to plants of *A. marginatus*, could explain the increased survivorship on *Brachiaria*. Plant tissue with lower fibre content could facilitate initiation of feeding by newly hatched nymphs. Increases in the amount of lignin in plant tissues prevent cercopid nymphs from reaching feeding sites (Hoffman & McEvoy, 1986). Differences in plant growth and architecture may also influence nymphal establishment. Because *B. decumbens* has a decumbent, stoloniferous growth habit and *A. marginatus* is a tall-growing grass with a tussock habitat (Klink, 1994), plants of *B. decumbens* can provide more sites for feeding and more protection to nymphs against desiccation. In addition, the pattern of nymphal survivorship observed in the field on caged and noncaged plants of *A. marginatus* and *B. decumbens* showed some indications that plants of *B. decumbens* could also protect the nymphs against natural enemies (Pires, 1998).

Spittlebug nymphs showed better survivorship on non water-stressed plants of *Brachiaria* and on fertilised plants of *A. marginatus* than on water-stressed and nonfertilised plants of these two host plants, respectively (Figs 5 and 6a). Negative effects of experimental water stress and positive effects of plant fertilisation have been reported in the majority of studies of sucking insects (Waring & Cobb, 1992). The high mortality of newly hatched nymphs reared on the low-water treatments could be a direct consequence of plant quality or could be due to the unfavourable microclimate around the plants. Newly hatched nymphs may not be able to initiate feeding on stressed plants, or they might die before reaching the plants and establishing a feeding site. When the newly hatched nymphs search for feeding sites, they are vulnerable to desiccation. The high survival of newly hatched nymphs on experimental non water-stressed plants accords with studies of the effect of moisture on changes in spittlebug population in the Federal District of Brazil. These studies indicate that low precipitation and a delay in the beginning of the rainy season have an adverse effect on survivorship of eggs and first-instar nymphs (C. S. S. Pires *et al.*, unpublished). The amount of rain and the frequency of the rains are important factors in the mortality of newly hatched nymphs.

It has been argued that for insect species where there is a strong linkage between preference and performance, the reproductive response of females to host plant quality is the critical factor regulating population densities (Price & Clancy, 1986; Craig *et al.*, 1989) and should be incorporated into life-table analyses (Preszler & Price, 1988). According to Preszler and Price (1988), the life tables for these phytophagous insects should start with the cohort of eggs in the female ovary and include the effect of host-plant quality in reducing this cohort of eggs in the female to the cohort of eggs actually oviposited. Evidence indicates that, for *D. flavopicta*, a species that shows eruptive characteristics on introduced grasses, the influences of natality and female oviposition behaviour in response to plant quality are not the major factors driving population outbreaks.

is case, the appropriate start of the life table may well be cohort of eggs laid in the soil.

The study reported here represents the first experimental validation of the Phylogenetic Constraints Hypothesis for a real insect species. Comparative studies on latent and eruptive species in tropical systems, as described above, are needed for the development of a broad, empirically based theory of insect population dynamics. The Phylogenetic Constraints Hypothesis is pluralistic because it uses divergent evolutionary background to explain the different patterns observed in insect population dynamics (Price, 1996).

Acknowledgements

I thank Evelyn Marques, Ana Goodman, and Edison Sujii for helpful comments that greatly improved this manuscript. I thank the field and laboratory work of the technician João P. Paes and the following students of the Ecology Laboratory at EMBRAPA/CENARGEN: Christhinne Andrade, Cristiane Oliveira, Cristiane Sardinha, Andrea Lini, Fernanda Gangana, and Cleber Annunziatto. This research was funded in part by a grant from the U.S. National Science Foundation (DEB-9318188), and in part by a grant from Conselho Nacional de Pesquisa e Desenvolvimento Científico e Tecnológico (CNPq/Brazil - 522315/94). Support for research in Brazil was provided by the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). This work was completed in partial fulfilment for the requirements of a PhD by C. S. S. Pires at Northern Arizona University.

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Accepted 26 May 1999

Dry-Season Embryonic Dormancy in *Deois flavopicta* (Homoptera: Cercopidae): Roles of Temperature and Moisture in Nature

CARMEN S. S. PIRES,¹ EDISON R. SUJII,¹ ELIANA M. G. FONTES,¹ CATHERINE A. TAUBER,² AND MAURICE J. TAUBER²

Environ. Entomol. 29(4): 714-720 (2000)

ABSTRACT A field-based experimental study examined the roles of temperature and moisture in the dry-season embryonic dormancy and postdormancy hatching of the spittlebug *Deois flavopicta* Stål from Brazil's dry interior region. The results show that dormancy consists of two discrete parts: an initial period of diapause that persists from April to the beginning of July, followed by a period of postdiapause quiescence that prevails until the rainy season begins (usually October). Low temperatures during the early part of the diapause period accelerates diapause development, whereas contact with liquid water determines the timing of postdiapause hatching. Soil temperatures during June and July and the relative humidity of the soil during August and September strongly affect overwintering survival and thus are important in determining the size of the nymphal population after dormancy. The findings indicate that, like hibernation and aestivation in temperate-zone insects, dry-season dormancy in tropical insects is a dynamic state that is influenced by seasonal changes in key environmental factors.

KEY WORDS *Deois flavopicta*, dry-season dormancy, moisture, temperature, survival, egg diapause

SEASONAL FLUCTUATIONS in a number of environmental factors, primarily daylength, temperature, and moisture, provide the main proximal cues for insect seasonal cycles (Beck 1980, Denlinger 1986, Tauber et al. 1986, Danks 1987). Given that most research on insect phenology has emanated from the Temperate Zone, much of the literature has emphasized the seasonal responses of insects to changes in photoperiod and temperature. In contrast, responses to moisture have received considerably less attention and as a result are much less well understood (Tauber et al. 1986, 1994, 1998). This disparity is particularly unfortunate because the seasonal cycles of large regions of the globe are dominated by wet-dry cycles, with flushes of plant and animal growth, reproduction, and dispersal concentrated mainly around the rainy season.

The vast interior of central Brazil (Cerrado vegetation) provides an excellent example of such an area where climate is characterized by well defined cycles of wet (and warm) - dry (and cool) seasons. During the dry-cool period (June through August), low moisture, low temperature, and lack of appropriate food cause major interruptions in insect life cycles. The resumption of growth, development, and reproduction is synchronized with the return of the wet-warm season. In this regard, we asked the following questions: Do insects that undergo dry-season dormancy exhibit dynamic patterns of responses to seasonal cues

that parallel those of the cold-season dormancy of temperate-zone insects (see Tauber et al. 1986, Chapter 3)? Or, is dry-season dormancy based on a simple set of responses (e.g., drought-induced quiescence that terminates upon exposure to moisture)?

To help answer these questions, we examined the dry-season dormancy of *Deois flavopicta* Stål, a grass-feeding insect endemic to midwestern and southeastern regions of Brazil. This insect can cause severe economic damage to pastures used for cattle raising and in central Brazil it withstands the dry season by entering diapause as eggs in the soil. The dry-season diapause serves to synchronize the insect's annual life cycle with that of its host-plants, which themselves are keyed to the rainy season (Fontes et al. 1995). Rain stimulates regrowth and favors production of new tissue in the hosts, thus providing tender, nutritious stems and leaves during the development of *D. flavopicta* nymphs and adults (Koller and Honer 1994, Pires 1998).

Eggs of nondiapausing *D. flavopicta* typically hatch within 16 d of oviposition (Fontes et al. 1995). In contrast, when eggs enter dry season dormancy, development is curtailed at the beginning of embryonic development, before tissue differentiation, when the zygotic nucleus is visible under the stereoscopic microscope (Koller et al. 1987). Hatching of diapausing eggs may take 61 to 360 d to occur. Although the factors that induce diapause in eggs laid before the dry season are unknown, earlier laboratory-based studies (Fontes et al. 1995, Sujii et al. 1995, Sujii 1998) showed that dormancy in *D. flavopicta* has two distinguishable periods: diapause followed by postdiapause quies-

¹ Empresa Recursos Genéticos e Biotecnologia, Cx. Postal 02372, Brasília, DF, 70849-970, Brazil.

² Department of Entomology, Cornell University, Comstock Hall, Ithaca, NY 14853-0901.

cence. They also indicated that low temperature can influence diapause development (=physiological processes leading to the termination of diapause), and that moisture is required for postdiapause development or hatch. Photoperiod has not been shown to have an effect on either period. These earlier results nurtured the current study, which focused on characterizing the dynamic seasonal patterns of egg responses to two major physical factors, temperature and moisture.

This investigation was designed to determine both the timing of the action as well as the function of these two physical factors during dry season dormancy. We sought to answer the following five questions: (1) When do the two periods of *D. flavopicta* dormancy (diapause and postdiapause quiescence) occur in nature? (2) When does low temperature influence the maintenance or termination of dormancy in nature? (3) When does moisture stimulate development in dormant eggs? (4) Does temperature influence survival during dormancy, and if so when? (5) Does water vapor (relative humidity) influence survival during dormancy, and if so when? Our approach was to monitor the seasonal responses of field-collected eggs of *D. flavopicta* to moisture and temperature at regular intervals throughout the dry-cool season, and to relate our findings to population levels of postdormancy nymphs in the field.

Materials and Methods

To determine when soil moisture and temperature influence dormancy in the spittlebug, we conducted a two-part experimental study. The first part began on 1 June and examined whether temperature or moisture hasten diapause development relatively early during the dry-cool season dormancy. During the second part, which began after the dry-cool season had progressed (1 July), we made monthly tests of the responses of dormant eggs solely to moisture. Following Tauber et al. (1990), we used the characteristics of hatch pattern to elucidate the effects of the various treatments on the progression of dormancy. However, in the case of *D. flavopicta*, the time for hatch to occur was calculated after eggs were provided with liquid water and high temperature (28°C), conditions known to promote hatch in nondiapause and postdiapause eggs (Fontes et al. 1995). Finally, we related our findings to the levels of nymphal populations immediately after the dry-season ended.

Egg Source and Handling. At the end of the rainy season (April), during the third generation of *D. flavopicta*, adults were caged for 15 d in a pasture area cultivated with *Brachiaria decumbens* Staf (Cranginea). The site was located ~40 km north of Brasília (DF), 15° 35' S, 47° 42' W; 1,000 m altitude. Females oviposited directly into the soil or litter of the pasture. During this period, any adults that died were replaced. Subsequently, the cages were removed and the oviposition sites were marked so the eggs could be recovered at appropriate times during the dry season.

To collect *D. flavopicta* eggs, samples of soil were sieved and immersed in a saturated salt solution (NaCl 40% WV). After 40 min, the flotation layer was collected and examined for eggs. Eggs were transferred from the flotation solution to uncovered plastic petri dishes containing a layer of cotton covered with filter paper. The petri dishes were then placed inside desiccators containing saturated salt solutions to maintain the relative humidity conditions (Winston and Bates 1960). The desiccators were kept inside environmental chambers at 15 or 28°C. When the experiment called for contact water, water was added to the cotton and filter paper. The photoperiod for all treatments was 12:12 (L:D) h. For each monthly sample (June–September), we included a control in which dormant eggs were exposed to liquid water at 28°C immediately after collection from the field.

Each treatment within each sample period consisted of a total of 60 eggs equally distributed among four replicates. The eggs were checked weekly until hatch or death of the embryo. For each treatment we calculated: percentage survival and time to hatch (from the date of contact with liquid water).

Treatments: June Sample. Dormant eggs that had been collected from the field on 1 June were transferred to four combinations of relative humidity and temperature conditions in the laboratory (see Table 1): low relative humidity (10–20%) and cool (15°C): high relative humidity (90–100%) and cool (15°C): low relative humidity (10–20%) and warm (28°C): high relative humidity (90–100%) and warm (28°C). After 1, 2, 3 or 4 mo, the eggs were transferred to warm conditions (28°C) under two relative humidity treatments: low (10–20%) and high (90–100%).

Treatments: July, August, and September Samples. Eggs collected in the field on 1 July, 1 August, and 1 September were subjected, for varying periods, to low (10–20%) and high (90–100%) relative humidity under warm conditions (28°C) (see Tables 2–4). At the end of the relative humidity treatments, the eggs were brought into contact with liquid water at 28°C.

Finally, on 16 August when >50% hatch was observed in the controls, all eggs from high relative humidity treatments of June, July, and August were placed in contact with liquid water at 28°C.

Nymph Population Level and Whether Data. Nymphs were sampled in October and November of 1990, 1991, 1992, and 1993, during the first generation. In a pasture area located ~40 km north of Brasília (DF), 15° 35' S, 47° 42' W; 1,000 m altitude. Once a week, we randomly sampled 50 quadrats of 0.25 by 0.25 m each, counting every individual present in the quadrat. A portable weather station was installed in the study area, from which we collected data on soil temperature and rainfall during the study period.

Statistics and Voucher Specimens. To analyze trends in hatching patterns, our statistics included the Mann-Whitney rank sum test for pairwise comparisons and the Kruskal-Wallis test for multiple comparisons or the parametric analysis of variance (ANOVA) followed by Student-Newman-Keuls for comparisons among means (Sokal and Rohlf 1995). We used the

Table 1. Survival and time for hatching (mean $\pm$ SD) in relation to temperature, relative humidity, and liquid water for samples of *D. flavopicta* eggs collected from overwintering field sites during June

Treatment	Condition I, d	Condition II, d	Time of transfer to liquid water, d	% hatch ^a (replicates/treatment = 4)	Time to hatch ^b (no. of eggs), d
1	CL (0-30)	WH (31-70)	70	38.8 $\pm$ 20.1cd	21.6 $\pm$ 8.2 (22)bcd
2	CL (0-30)	WL	—	0	—
3	CL (0-60)	WH (61-70)	70	60.3 $\pm$ 6.4bc	17.4 $\pm$ 1.7 (33)d
4	CL (0-60)	WL	—	0	—
5	CL (0-90)	—	90	30.5 $\pm$ 16.9de	26.3 $\pm$ 7.6 (18)ab
6	CL (0-90)	WL	—	0	—
7	CL (0-120)	—	120	16.8 $\pm$ 8.5de	34.0 $\pm$ 10.9 (10)a
8	CL (0-120)	WL	—	0	—
9	CH (0-30)	WH (31-70)	70	8.5 $\pm$ 6.0e	13.2 $\pm$ 9.3 (5)e
10	CH (0-30)	WL	—	0	—
11	CH (0-60)	WH (61-70)	70	72.3 $\pm$ 12.8b	23.4 $\pm$ 12.7 (45)bc
12	CH (0-60)	WL	—	0	—
13	CH (0-90)	—	90	62.5 $\pm$ 15.1bc	24.3 $\pm$ 10.2 (36)b
14	CH (0-90)	WL	—	0	—
15	CH (0-120)	—	120	90.0 $\pm$ 6.7a	20.0 $\pm$ 0 (56)
16	CH (0-120)	WL	—	0	—
17	WL (0-30)	WH (31-70)	70	40.5 $\pm$ 17.6de	17.7 $\pm$ 8.7 (19)c
18	WL (0-30)	WL	—	0	—
19	WL (0-60)	WH (61-70)	70	19.5 $\pm$ 9.5de	19.6 $\pm$ 8.4 (11)bcd
20	WL (0-60)	WL	—	0	—
21	WL (0-90)	—	90	0 (55)	—
22	WL (0-90)	WL	—	0	—
23	WL (0-120)	—	120	0	—
24	WL (0-120)	WL	—	0	—
25	WH (0-30)	WL	—	0	—
26	WH (0-30)	WH (31-70)	70	27.5 $\pm$ 11.4de	26.1 $\pm$ 10.6 (14)ab
Control	—	—	0	62.2 $\pm$ 11.9	54.3 $\pm$ 11.1 (57)

^a Numbers followed by the same letters are not significantly different (ANOVA: $F = 16.08$; $df = 10, 33$; $P < 0.001$ and Student-Newman-Keuls test, $P < 0.05$).

^b Original data; for statistic analyses data were transformed using $\ln$. Numbers followed by the same letters are not significantly different (ANOVA: $F = 8.15$; $df = 9, 206$; $P < 0.001$ and Student-Newman-Keuls test, $P < 0.05$).

computer program Sigmasat (Kuo et al. 1992). The relationship between physical factors in the field and postdormancy nymphal populations were assessed by eye. Voucher specimens are deposited in the Insect Collection of Embrapa Cerrados, Brasília, Brazil.

Results

The Progression of Dormancy. Dormant eggs laid in April, collected early in the dry-cool season (1 June), and incubated in the laboratory under conditions that

promote development (high temperature, 28°C, and contact with liquid water) did not begin hatching until the middle of July (Table 1, control). Time for eggs to hatch after exposure to liquid water decreased significantly from June to July, from July to August, and remained constant between August and September (Kruskal-Wallis, $H = 149.3$, $df = 3$, $P < 0.001$; Dunn test, $P < 0.05$; Fig. 1, Fig. 2).

These data confirm that dormancy in *D. flavopicta* eggs has, at least, two distinct parts: diapause and postdiapause quiescence. The first period (diapause),

Table 2. Survival and time for hatching (mean $\pm$ SD) of *D. flavopicta* eggs in relation to relative humidity and liquid water for samples collected from overwintering field sites during July (Temp = 28 $\pm$ 2°C)

Treatment	Condition I, d	Condition II, d	Time of transfer to liquid water, d	% hatch (replicates/treatment = 4)	Time to hatch (no. of eggs), d
27	L (0-30)	H (31-42)	42	63.3 $\pm$ 32.4	19.0 $\pm$ 6.0 (28)
28	L (0-60)	—	60	0	—
29	L (0-90)	—	90	0	—
30	L (0-120)	—	120	0	—
31	L (0-60)	—	—	0	—
32	L (0-90)	—	—	0	—
33	L (0-120)	—	—	0	—
34	H (0-30)	L (31-300)	—	10.3 $\pm$ 2.6	27.5 $\pm$ 8.6 (6)
35	H (0-42)	—	42	15.5 $\pm$ 13.0	21.0 $\pm$ 1.9 (8)
36	H (0-42)	—	42	6.0 $\pm$ 4.9	16.8 $\pm$ 4.5 (4)
Control	—	—	0	83.5 $\pm$ 11.6	23.2 $\pm$ 5.6 (51)

L, low relative humidity (10-20%); H, high relative humidity (80-90%)

Table 3. Survival and time for hatching (mean $\pm$ SD) of *D. flavopicta* in relation to relative humidity and liquid water for samples collected from overwintering field sites during August (Temp = $28 \pm 2^\circ\text{C}$)

Treatment	Condition, d	Time of transfer to liquid water, d	% hatch (replicates/treatment = 4)	Time to hatch (no. of eggs), d
37	L (0-30)	30	0	—
38	L (0-60)	60	0	—
39	L (0-90)	90	0	—
40	L (0-30)	—	0	—
41	L (0-60)	—	0	—
42	L (0-90)	—	0	—
43	L (0-120)	—	0	—
44	H (0-9)	9	91.8 $\pm$ 10.5	24.4 $\pm$ 13.2 (32)
Control	—	0	88.5 $\pm$ 23.8	19.4 $\pm$ 2.2 (69)

L, low relative (10–20%) humidity; H, high (80–90%) relative humidity.

which persists at least throughout the early part of June, is characterized by a relatively low incidence of hatching and a long incubation period (more than ~30 d) after exposure to liquid water (Table 1, control). In contrast, during the second period of dormancy (quiescence, after 1 July), eggs hatch promptly (within an average of 19 d) after coming into contact with water (Tables 2–4, controls).

Response to Liquid Water. Our results confirm previous findings that eggs have a significant response to contact water during the second period of dormancy (after 1 July). In general, when eggs were not stressed (e.g., exposed to warm, dry conditions) during quiescence, the percentage of hatching was high (>63%) and hatching occurred quickly (within ~20 d) after exposure to liquid water (e.g., Table 2, control and treatment 27; Table 3, control and treatment 44; Table 4, control). In contrast, virtually no eggs hatched in treatments from the same months (August and September) that were not exposed to water (e.g., Table 2, treatments 31–34; Table 3, treatments 40–43; Table 4, treatments 49–52).

Similarly, no hatch was observed in treatment 16 from the June sample, which was exposed to warm conditions but not to liquid water after having experienced 120 d under cool and high relative humidity conditions; whereas, the eggs in treatment 15, which were exposed to equivalent conditions for 120 d and then given liquid water, showed a very high rate (90%) of hatching (Table 1). The only exception to this

pattern occurred in treatment 34 from July; however, eclosion in this group was limited to 10%.

Response to Temperature: 1 June Sample. Given previous findings (Sujii et al. 1995), we had expected low temperatures to hasten diapause development during the first period of dormancy (June and early July). This was not the case. For eggs removed from the field in June, the temperature conditions applied during the first 60 d after collection did not influence the time for hatching after exposure to contact water (warm versus cold conditions) (treatment 1 versus 17 [$t = -1.458$, $df = 39$, $P > 0.05$]; treatment 3 versus 19 [$t = -1.392$, $df = 42$, $P > 0.05$]; treatment 11 versus 26 [$t = 0.741$, $df = 57$, $P > 0.05$]; Table 1).

Response to Relative Humidity During Dormancy. Eggs collected during the first period of dormancy (1 June) and then subjected to either high or low relative humidity during the first 2 mo (days 0–60) did not show significant variation in either the incidence of hatching or the time for hatching after exposure to contact water (treatments 1, 3, 9, 11, 17, 19, and 26; Table 1). However, when eggs experienced high relative humidity during the third and fourth months (days 90–120), the incidence of hatching was higher than in eggs that experienced low relative humidity (treatment 5 versus 13 [$t = 2.83$, $df = 6$, $P < 0.05$]; treatment 26 versus 15 [$t = 14.59$, $df = 6$, $P < 0.05$]; Table 1). Overall, for the 1 June sample, the combination of low temperature during the first 2 mo (days 0–60) and high relative humidity in the last 2 mo (days

Table 4. Survival and time for hatching (mean $\pm$ SD) of *D. flavopicta* in relation to relative humidity and liquid water for samples collected from overwintering field sites during September (Temp = $28 \pm 2^\circ\text{C}$)

Treatment	Condition, d	Time of transfer to liquid water, d	% hatch (replicates/treatment = 4)	Time to hatch (no. of eggs), d
45	L (0-30)	30	0	—
46	L (0-60)	60	0	—
47	L (0-90)	90	0	—
48	L (0-120)	120	0	—
49	L (0-30)	—	0	—
50	L (0-60)	—	0	—
51	L (0-90)	—	0	—
52	L (0-120)	—	0	—
Control	—	0	67.8 $\pm$ 15.6	19.6 $\pm$ 14.3 (25)

L, low relative humidity (10–20%); H, high relative humidity (80–90%).

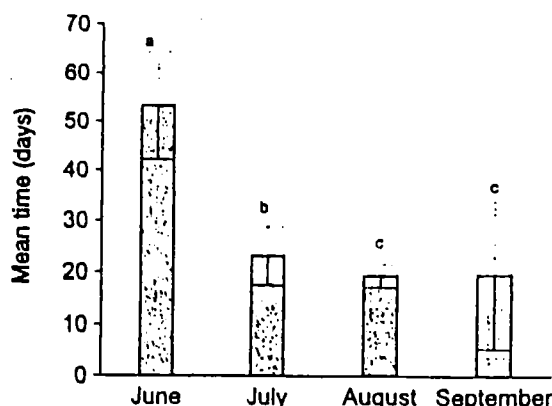


Fig. 1. Comparisons of the time for hatching of *D. flavopicta* eggs collected from overwintering sites during the dry season in Brasilia, DF, Brazil, and exposed to contact water at 28°C directly after collection from the field. Bars (mean $\pm$ SD) with different letters differ significantly (Kruskal-Wallis ANOVA on ranks, $H = 149.3$, $P < 0.001$, Dunn test, $P < 0.05$).

61–120) (treatments 3, 11, 13, 15; Table 1) produced significantly higher eclosion levels ($>60\%$) than all other combinations of conditions (ANOVA; $F = 16.08$; $df = 10, 33$; $P < 0.001$ and Student-Newman-Keuls, $P < 0.05$; Table 1).

Eggs that remained in the field during August and that were then subjected to contact moisture on 1 September showed a lower and more variable rate of hatch than those that were transferred to contact moisture during the early part of August (Table 4, control versus Table 3, treatment 44 and control). Eggs that were transferred from the field on 1 August or 1 September and then subjected to low relative humidity and high temperature conditions for 30 or more days suffered 100% mortality (Table 3, treatments 37, 38).

Nymphal Population Trends. There were marked differences among the 4 yr (1990–1993) that we studied the occurrence and size of postdormancy nymphal populations. During 2 of the 4 yr (1990 and 1991), temperatures were low ($<19^\circ\text{C}$) (Fig. 3). In one of these years (1991), the rains began at the end of September and persisted without major interruption for at least 2 mo. The population level after this dry season (1991) was high. In 1990, the rains began early (end of July), but they were interrupted for 5 wk during August and early September. The population level at the end of dormancy that year was very low.

During the next 2 yr (1992 and 1993, both El Niño years), temperatures during the dry-“cool” season were relatively high (Fig. 4). In 1992, the weekly average minimum temperature ranged between 19 and 23°C ; in 1993 it did not fall below 22°C . Postdormancy nymphal populations were low in both years, especially in 1993 when rainfall was also erratic.

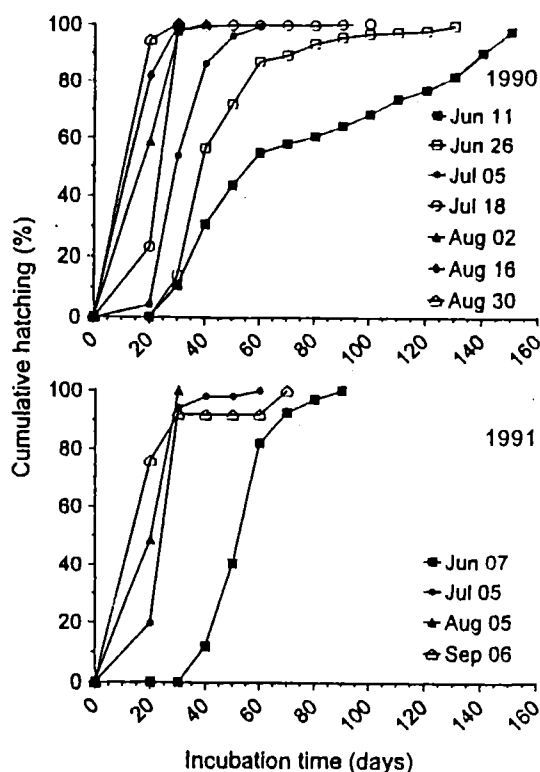


Fig. 2. Pattern of hatching of the spittlebug, *D. flavopicta*, eggs collected from overwintering sites during the dry season in Brasilia, DF, Brazil (June–August in 1990 and June–September in 1991). Eggs were exposed to contact water at 28°C directly after collection from the field.

Discussion

Our results demonstrated that the dry-cool season dormancy in the tropical insect *D. flavopicta* shares many features with the hibernation diapause that is characteristic of many Temperate Zone insects. For example, dormancy in most Temperate Zone insects comprises two dynamic parts—an early period of diapause that precedes a period of postdiapause quiescence. In *D. flavopicta*, diapause persists in most members of the population until the beginning of July; subsequently postdiapause quiescence prevails until the rainy season begins. Our results also demonstrate that physical conditions (temperature and moisture) can strongly influence both the timing and the size of the first generation of *D. flavopicta* after dormancy.

Temperature and Diapause Maintenance. Earlier reports showed that low temperatures applied to *D. flavopicta* eggs very early during diapause (mid-April) hastened the termination of diapause (Sujii et al. 1995). For example, eggs that experienced 64 day/night cycles of $23/15^\circ\text{C}$ in the presence of contact moisture, hatched within <50 d, whereas those that remained under constantly warm conditions (with contact water) required ~ 140 d for hatching.

In contrast, low temperature did not enhance the rate of diapause development in the eggs that we tested

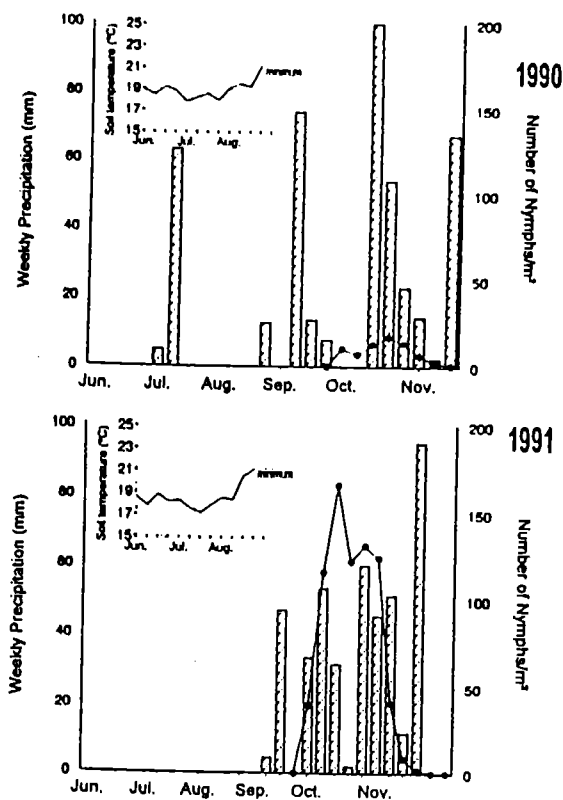


Fig. 3. Average weekly soil temperature, weekly precipitation, and population levels of *Deols flavopicta* nymphs (1990–1991) in Brasília, DF, Brazil

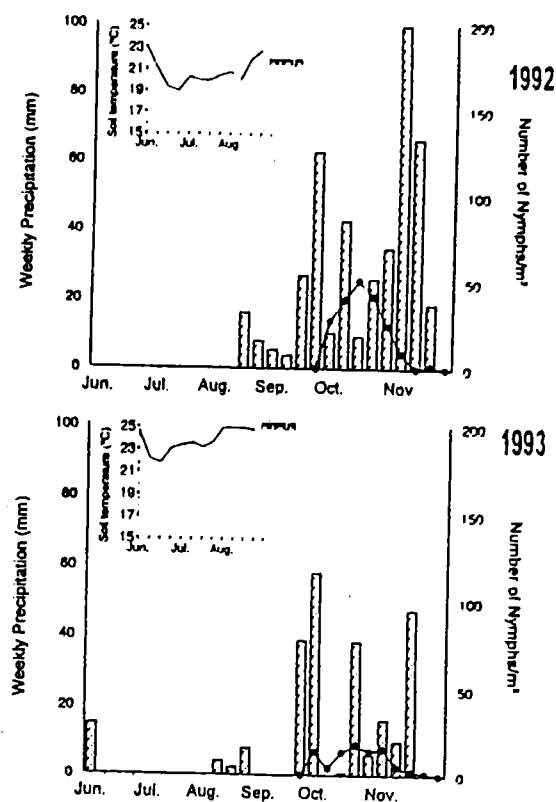


Fig. 4. Average weekly soil temperature, weekly precipitation, and population levels of *D. flavopicta* nymphs (1990–1991) in Brasília, DF, Brazil.

during June (Table 1). The different results from the two studies demonstrate that between April and June the thermal threshold for diapause development rises, and that by June it approximates the nondiapause level. Thus, diapause in our June samples ended as quickly under warm conditions as it did under cool conditions. This finding underscores the conclusion that, in common with hibernial and aestival diapause in Temperate Zone insects, dry-season diapause in tropical insects undergoes dynamic changes. In Temperate-Zone insects, these changes proceed in a characteristic and predictable fashion that can be measured by a very distinct, seasonally timed progression in thermal, photoperiodic, and other responses (e.g., Tauber et al. 1982, 1986, 1990), and it appears that this progression occurs in dry-season dormancy as well.

An intriguing question remains: How do the seasonal changes in *D. flavopicta*'s responses to temperature function during diapause? Do they act to maintain or terminate diapause? The temporal relationship between the seasonal changes of the soil temperature in the field and the seasonal progression of *D. flavopicta*'s responses to temperature indicates that temperature acts primarily at the beginning of the dry season to decelerate the rate of diapause development and thus maintain diapause. That is, *D. flavopicta*'s thermal optimum for diapause development is lowest

at the beginning of the dry-cool season (approximately April) when the soil is still warm. Thus, the rate of diapause development slows and diapause persists. As the dry-cool season progresses and the soil becomes consistently cool, the insect's thermal optimum for diapause development moves upward; again, diapause development decelerates and diapause persists. Finally, diapause ends, apparently spontaneously (without an external stimulus), in the middle of the dry-cool season (1 June–1 July in ~87% of the population) (Fig. 4), when there is a low probability that sufficient contact moisture would occur to stimulate premature development.

Postdiapause Quiescence and Liquid Water. *D. flavopicta* eggs, like the eggs of many insects, require contact with water before they hatch. In some species, water absorption occurs before or during egg diapause; in others it occurs only after diapause has been completed (see Ando 1972). *D. flavopicta*, falls into the latter category. Liquid water stimulated hatching only during quiescence (after July); it did not enhance the rate of diapause development, which occurs before July. Nondiapause eggs have a similar requirement for contact with free water before they hatch (Fontes et al. 1995).

In *D. flavopicta*, the moisture requirement for the initiation of postdiapause as well as nondiapause development is not satisfied by high (90–100%) relative hu-

midity (Tables 1 and 2); rather, liquid moisture appears to be necessary. In this respect, *D. flavopicta* eggs resemble the eggs of many species of insects (see Hinton 1981), but they differ from those of the tropical walking stick *Extatosoma tiaratum* (Macleay), which can absorb atmospheric water (Yoder and Denlinger 1992).

Survival During Dormancy: Environmental Determinates. In laboratory experiments, survival during dormancy was consistently associated with at least two factors: cool conditions during late diapause (June, July, and perhaps August), and high levels of relative humidity during quiescence (August onward). Thus, the insects' responses to low temperature during dormancy appear to serve two functions: to maintain diapause before and during the very early parts of the dry-cool season (see above) and to conserve metabolic reserves during the later parts of the dry-cool season. Our experiments did not examine the significance of temperature after July; however, we suspect that continued low temperatures until the beginning of the rainy season would enhance the rates of hatch after dormancy.

The above interpretation of our laboratory results, relative to temperature, is consistent with both the timing and incidence of nymphal occurrence in relation to soil temperature and rainfall in the field over the 4 yr that we studied. Postdormancy nymphal population levels (and presumably embryonic survival) were high during only 1 yr—the 1 yr in which temperatures were relatively low during the dry season and subsequent rainfall persisted. In contrast, nymphal population levels (and presumably embryonic survival) were low in the other 3 yr—each of which had a relatively warm dry season or erratic or low levels of rainfall after the dry season.

Given our results, we propose that postdormancy *D. flavopicta* populations will be large following dry seasons that are relatively cool and when the wet-season rains occur early and without significant interruption. Such information is crucial for promoting rational decisions for managing this economically important pest. However, it should be noted that population levels of nymphs early in the rainy season provide only indirect estimates of survival during embryonic dormancy. Thus, our results provide a sound basis for developing a quantitative predictive model and for efficiently gathering appropriate data to verify the model.

Acknowledgments

We thank João S. O. Paes and Dagoberto Gomes for help with the field and laboratory work. We acknowledge the financial support of Conselho Nacional de Pesquisa e Desenvolvimento Científico e Tecnológico (CNPq/Brazil-522315/94.1), and National Science Foundation Grant INT-9817231, and Regional Project W-185.

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Received for publication 7 July 1999; accepted 22 March 2000.

Spittlebug indicators of nitrogen-fixing plants

VINTON THOMPSON School of Science and Mathematics, Roosevelt University,
Chicago, Illinois, U.S.A.

Abstract. 1. Spittlebugs (Homoptera: Cercopoidea) are preferentially associated with nitrogen-fixing angiosperms. Generally, the Aphrophoridae associate with legumes, the Clastopteridae with actinorhizal plants, and the Cercopidae with associative nitrogen-fixing grasses. This is the first reported insect–host association specific to nitrogen-fixing plants.

2. It is probable that spittlebugs are attracted to nitrogen-fixing plants because these hosts provide a relatively rich, reliable source of organic nitrogen compounds for xylem-sucking insects.

3. Many spittlebugs live on plants that do not fix nitrogen, and ecological, mechanical or chemical factors may bar some spittlebugs from otherwise suitable nitrogen-fixing plants.

4. Among nitrogen-fixing hosts, spittlebugs appear to prefer plants that transport fixed nitrogen as amino acids and amides to plants that transport fixed nitrogen as ureides.

Key words. Spittlebugs, Cercopoidea, xylem feeding, nitrogen-fixing plants, actinorhizal plants, associative nitrogen fixation, ureides, sugar cane, tropical pasture grasses.

Introduction

Insects may serve as useful guides to taxonomically diverse host plants which share a common chemical ecology. Danaid butterflies, for example, associate with cardiac glycoside-bearing hosts scattered among several plant families (Ackery & Vane-Wright, 1984). While studying spittlebug ecology I was struck by heavy infestations on two sets of commonly recognized nitrogen-fixing hosts, leguminous forage crops and alders (Thompson & Halkka, 1973; Thompson *et al.*, 1987). More extensive investigation disclosed an unexpectedly broad association between spittlebugs and a diverse collection of nitrogen-fixing hosts. Here I document this association, propose a likely physiological basis, and draw implications for agriculture and the discovery of novel nitrogen-fixing plants. So far as I am aware, this is the first reported insect–host association peculiar to nitrogen-fixing plants.

Almost 80% of the atmosphere is nitrogen, but eukaryotes cannot assimilate nitrogen gas (N_2). Consequently, nitrogen is a limiting ecological factor for many plants and

herbivores (Mattson, 1980). Some angiosperms meet all or a portion of their nitrogen requirements through transfer of fixed nitrogen from root-borne prokaryotic partners (Sprent & Raven, 1992). Most legumes (Leguminosae) and trees of the small tropical genus *Parasponia* (Ulmaceae) form root nodule symbioses with nitrogen-fixing bacteria of the genera *Rhizobium* or *Bradyrhizobium* (Sprent & Raven, 1992). A taxonomically eclectic group of non-leguminous woody dicots, collectively known as actinorhizal plants, form similar associations with nitrogen-fixing bacteria of the genus *Frankia* (Bond, 1983; Baker & Mullin, 1992). A few plants, primarily grasses, form looser root associations with a variety of bacteria and obtain a substantial portion of their nitrogen from rhizospheral or 'associative' nitrogen fixation (Döbereiner & Pedrosa, 1987; Miranda & Boddey, 1987; Boddey & Döbereiner, 1988; Elmerich *et al.*, 1992; Urquiaga *et al.*, 1992).

Spittlebugs (Homoptera: Cercopoidea) are medium-sized plant-sucking insects with about 2380 species worldwide (Hodkinson & Casson, 1991) divided among four families (Metcalf, 1962). The largest families are the Cercopidae, primarily tropical, and the Aphrophoridae, most abundant in temperate areas but well represented in the tropics. The small family Clastopteridae is essentially monogeneric and, with the exception of two species in

Correspondence: Dr V. Thompson, School of Science and Mathematics, Roosevelt University, 430 South Michigan Avenue, Chicago, IL 60605, U.S.A.

the Philippines, confined to the Americas. The family Machaerotidae is found in Africa, Australia and southern Asia.

Most spittlebugs are oligophagous or polyphagous (Hodkinson & Casson, 1991). The common north temperate spittlebug *Philaenus spumarius* (L.) has almost 500 documented host plants, more than any other insect (Weaver & King, 1954; Halkka *et al.*, 1967; Owen, 1988; Holopainen & Varis, 1991), and many other spittlebugs have long host lists. Spittlebugs apparently tolerate a wide variety of hosts because the nymphs and most adults feed on xylem sap, an unusual food source and one relatively free from the chemical defences common in phloem sap and other plant parts (Raven, 1983; Owen, 1988). Aphrophorid, clastopterid and cercopid nymphs dwell in characteristic 'spittle masses' formed by adding small bubbles and a mucopolysaccharide to excreted xylem sap (Marshall, 1966). Machaerotid nymphs dwell in small, liquid-filled tubes (Maa, 1963), with the 'spittle' stage limited to the last moult. The spittles and dwelling tubes highlight the presence of nymphs and facilitate host plant studies. Adult spittlebugs do not form spittle masses.

The distribution of spittlebugs on nitrogen-fixing plants

Despite their catholic tastes, spittlebugs show a pronounced affinity for nitrogen-fixing plants. The details vary with family. In general, the Aphrophoridae are preferentially associated with legumes, the Clastopteridae with actinorhizal plants, and the Cercopidae with associative nitrogen-fixing grasses. Whereas these associations are far from exclusive, they are common, widespread and economically significant.

Many spittlebugs of the family Aphrophoridae prefer legume hosts. The highly polyphagous meadow spittlebug *Philaenus spumarius* favours herbaceous legumes and reaches pest status (Table 1) on nitrogen-fixing forage crops such as *Medicago sativa* (L.) and *Trifolium pratense* (L.) (Weaver & King, 1954; Halkka & Halkka, 1990). The polyphage *Lepyronia coleoptrata* (L.) and a Pakistani species of *Ptyelus* also favour herbaceous legumes (Rishi & Khan, 1986; Wheeler, 1991). Nymphs of the American spittlebugs *Aphrophora fulva* (Doering) and *Philaronia abjecta* (Uhler) favour *Lupinus* hosts (Hamilton, 1982). Three abundant tropical spittlebugs, the Latin American species *Cephus siccifolius* (Walker), the African species *Ptyelus grossus* (Fallen) and the Madagascan species *Ptyelus goudoti* (Bennett), show a preference for leguminous trees such as *Erythrina* and *Acacia* (Licent, 1912; Williams, 1921; Torres, 1946; Owen & Wiegert, 1976; Callan, 1991).

Species of the genus *Clastoptera*, the only genus of consequence in the Clastopteridae, show a marked attraction to actinorhizal plants. They are preferentially associated with at least five of the twenty or so known actinorhizal genera (Table 2), including the widespread genera *Alnus*, *Myrica* and *Casuarina*. This association is statistically significant (see below).

Species of the family Cercopidae reach pest levels on most agriculturally significant tropical grasses with well-documented associative nitrogen fixation (Table 1). They are the most important threat to pasture productivity in Latin America and the southeastern United States (Fagan & Kuitert, 1969; Enkerlin & Morales, 1979; Centro Internacional de Agricultura Tropical, 1982; Valerio, 1988), as well as destructive pests of sugar cane in Trinidad, Mexico, Central and South America, and Australia (Williams, 1921; Fewkes, 1969; Magarey *et al.*, 1988). Cercopid spittlebugs also occur widely on the associative nitrogen-fixing tropical pasture grass *Paspalum notatum* (Flugge.). This New World species is apparently more resistant to spittlebug damage than the introduced Old World grasses that figure so prominently among the hosts of severe spittlebug pests (Table 1).

Some spittlebug nitrogen-fixing host associations fall outside the general pattern described above. The European cercopid polyphage *Cercopis sanguinolenta* (Scopoli) favours herbaceous legumes (Licent, 1912), whereas the aphrophorids *Aphrophora alni* (Fallén) and *A. saratogensis* (Fitch) prefer actinorhizal host plants (Table 2). The common Australian aphrophorid *Philagra parva* (Donovan) is found on *Casuarina* (Table 2) as well as leguminous acacias (Evans, 1966). *Philaenarcys spartina* (Hamilton), an endemic Canadian aphrophorid, prefers associative nitrogen-fixing grasses of the genus *Spartina* (Hamilton, 1982). Species of the aphrophorid genera *Poophilus* and *Aphrophora* are minor pests of sugar cane (Fewkes, 1969). *Clastoptera arizonana* (Doering) lives on *Acacia cardiophylla* (Johnson & Lyon, 1991). These cases suggest that the spittlebug predilection for nitrogen-fixing hosts is general and, given the right circumstances, may develop in any spittlebug group for any set of nitrogen-fixing hosts. There are two probable exceptions. Neither the Clastopteridae nor the Machaerotidae have been observed to feed on monocots (Maa, 1963, and unpublished review of the host literature by the author). It is unlikely that these spittlebugs occur on associative nitrogen-fixing grasses. Machaerotids have not been reported on any nitrogen-fixing plants.

The spittlebug nitrogen-fixing plant association is not coincidental

Several facts suggest that the spittlebug-plant associations described above are not coincidental. First, some of the most severe spittlebug infestations occur where native spittlebugs have encountered introduced nitrogen-fixing hosts. Spittlebugs have their greatest economic impact on sugar cane, signal grass, buffel grass, bermuda grass and pangola grass, all Old World nitrogen-fixing species that have acquired New World spittlebug pests (Table 1). Native spittlebugs of the genus *Clastoptera* heavily infest introduced Australian *Casuarina* trees throughout the West Indies (Table 2). *Ptyelus goudoti* occurs in immense numbers on the introduced tree *Acacia mollissima* (Willdenow) in Madagascar (Callan, 1991). Something intrinsic

Table 1. Angiosperm hosts with spittlebug pests, arranged by severity. Major damage implies long-term or widespread economic loss and a significant accompanying agronomic literature. Intermediate damage implies occasional severe damage or widespread and extended but less severe damage. Lesser damage implies significant damage limited in time or space. Several isolated reports of pest status have been omitted. There are also two well-documented spittlebug pests of conifers, *Haematoloma dorsatum* on pines in Italy (Covassi *et al.*, 1989) and *Aphrophora saratogensis* adults on *Pinus resinosa* (Ait.) in eastern North America (Hamilton, 1982). The actinorhizal plant *Comptonia peregrina* serves as a major nymphal host for *Aphrophora saratogensis* (Table 2), promoting pine infestation by the adults. (a) indicates that only adult spittlebugs live on the host. (i) indicates that the host plant is introduced in areas of serious infestation. With the possible exception of *Philaenus*, the spittlebug pests are native to areas of serious infestation. The spittlebug genera *Cephus*, *Clovie* and *Philaenus* belong to the Aphrophoridae. *Aeneolamia*, *Cosmoscarta*, *Deois*, *Mahanarva*, *Prosapia* and *Zulia* belong to the Cercopidae. For documentation of associative nitrogen fixation in grasses see Döbereiner & Pedrosa (1987), Miranda & Boddey (1987), Boddey & Döbereiner (1988) and Urquiaga *et al.* (1992). There is evidence that some *Pennisetum* spp. may also exhibit associative nitrogen fixation (Urquiaga *et al.*, 1992).

Host species	Common name	Nitrogen fixation?	Representative pest genera	References
A. major damage				
<i>Brachiaria decumbens</i>	Signal grass (i)	Associative	<i>Deois</i> , <i>Zulia</i> , <i>Aeneolamia</i>	1, 2, 3, 4, 5
<i>B. humidicola</i>	None (i)	Associative	<i>Deois</i> , <i>Zulia</i>	1, 5
<i>Cenchrus ciliaris</i>	Buffel grass (i)	—	<i>Aeneolamia</i> , <i>Prosapia</i>	4, 6
<i>Cynodon dactylon</i>	Bermuda grass (i)	Associative	<i>Aeneolamia</i> , <i>Prosapia</i>	6, 7, 8, 9, 10, 11
<i>Digitaria decumbens</i>	Pangola grass (i)	Associative	<i>Aeneolamia</i> , <i>Prosapia</i>	7, 8, 6, 12, 13
<i>Panicum maximum</i>	Guinea grass (i)	Associative	<i>Aeneolamia</i> , <i>Prosapia</i>	5, 6, 12, 13
<i>P. purpurascens</i>	Para grass (i)	—	<i>Aeneolamia</i> , <i>Prosapia</i>	11, 12
<i>Pennisetum clandestinum</i>	Kikuyu grass (i)	—	<i>Aeneolamia</i> , <i>Prosapia</i>	2, 14
<i>Medicago sativa</i>	Alfalfa (i)	Rhizobial	<i>Philaenus</i>	15, 33
<i>Saccharum officinalis</i>	Sugar cane (i)	Associative	<i>Aeneolamia</i> , <i>Mahanarva</i>	9, 13, 16, 17, 18
<i>Trifolium pratense</i>	Red clover (i)	Rhizobacous	<i>Philaenus</i>	15, 33
B. Intermediate damage				
<i>Carya illinoensis</i>	Pecan	—	<i>Clastoptera</i>	19
<i>Casuarina equisetifolia</i>	Australian pine (i)	Actinorhizal	<i>Clastoptera</i>	20
<i>Cynodon plectostachyus</i>	Star grass (i)	—	<i>Aeneolamia</i> , <i>Prosapia</i>	6
<i>Echinochloa polystachia</i>	Aleman grass	—	<i>Aeneolamia</i> , <i>Prosapia</i>	6, 12
<i>Fragaria</i> spp.	Strawberry (i)	—	<i>Philaenus</i>	21, 22
<i>Hyparrhenia rufa</i>	Jaragua grass	—	<i>Aeneolamia</i> , <i>Prosapia</i>	6, 12
<i>Lotus corniculatus</i>	Birdsfoot trefoil (i)	Rhizobial	<i>Philaenus</i>	23
<i>Oryza sativa</i>	Rice (i)	Associative	<i>Aeneolamia</i> , <i>Deois</i> (a)	5, 17, 18, 24
<i>Pennisetum purpureum</i>	Elephant grass (i)	—	<i>Aeneolamia</i> , <i>Prosapia</i>	6, 9, 12
<i>Stenotaphrum secundatum</i>	St. Augustine grass	—	<i>Prosapia</i>	7
<i>Theobroma cacao</i>	Cacao	—	<i>Clastoptera</i>	25, 26
C. Lesser damage				
<i>Atrocarpus integrifolius</i>	Jak	—	<i>Clovie</i> , <i>Cosmoscarta</i>	27, 28
<i>Casuarina stricta</i>	Australian pine (i)	Actinorhizal	<i>Clastoptera</i>	20, 29
<i>Chloris gayana</i>	Rhodes grass (i)	—	<i>Aeneolamia</i> , <i>Prosapia</i>	6, 9
<i>Erythrina crista-galli</i>	Coral tree	Rhizobial	<i>Cephus</i>	39
<i>Gossypium</i> spp.	Cotton	—	<i>Machaerota</i> , <i>Clastoptera</i>	25, 31, 32
<i>Ilex opaca</i>	American holly	—	<i>Prosapia</i> (a)	8, 11
<i>I. cornuta</i>	Burford holly (i)	—	<i>Prosapia</i> (a)	8
<i>Zea mays</i>	Maize	—	<i>Prosapia</i> , <i>Aeneolamia</i>	7, 18

References: 1 = Ferrufino & Lapointe, 1989; 2 = Centro Internacional de Agricultura Tropical, 1982; 3 = Valerio, 1988; 4 = Botelho *et al.*, 1985; 5 = Nilakhe, 1985; 6 = Enkerlin & Morales, 1979; 7 = Fagan & Kuitert, 1969; 8 = Pass & Reed, 1965; 9 = Filho, 1944; 10 = Barrientos, 1985; 11 = Mead, 1962; 12 = Coronado & Sosa, 1966; 13 = Oomen, 1975; 14 = Fagan & Picado, 1971; 15 = Weaver & King, 1954; 16 = Fewkes, 1969; 17 = Williams, 1921; 18 = Guagliumi, 1962; 19 = Polles, 1972; 20 = Bennett & Hughes, 1963; 21 = Halkka, 1940; 22 = Schaefer, 1981; 23 = Mackun & Baker, 1990; 24 = Golding, 1946; 25 = Mendes, 1979; 26 = Saunders, 1981; 27 = Ayyar, *et al.*, 1967; 28 = Fletcher, 1920; 29 = Mead & Bennett, 1987; 30 = Torres, 1946; 31 = Misra, 1920; 32 = Otañez & Butac, 1939; 33 = Halkka & Halkka, 1990.

to the biology of these hosts, independent of long-term host-parasite evolution, attracts spittlebugs. Whereas I cannot rule out the possibility that spittlebugs are drawn to nitrogen-fixing plants by correlated ecological or physio-

logical features, the only obvious trait these hosts share is nitrogen fixation.

Second, statistical analysis strongly supports the existence of an association between species of the genus

Table 2. Actinorhizal host plants with spittlebug associates. Includes only cases in which the host plant is the preferred host, or one of a few preferred hosts, for the spittlebug associate. *A. uva-ursi*, a suspected host of *A. corticea* nymphs (Ossiannilsson, 1981), may not be actinorhizal (Bond, 1967, 1983). Note that most spittlebugs of actinorhizal plants belong to the New World genus *Clastoptera* of the Clastopteridae. (a) indicates that only adult spittlebugs live on the host. (n) indicates that only nymphal spittlebugs live on the host. (i) indicates that the host plant is introduced. With the exception of *A. alni* in North America, the spittlebugs are native to the areas given. For documentation of actinorhizal plants see Bond (1967, 1983) and Baker & Mullin (1992). The *Clastoptera* hosts included in this list are excerpted from an unpublished list of 154 *Clastoptera* hosts compiled by the author (see text).

Actinorhizal host plant	Spittlebug associate	Geographical area	Reference
<i>Alnus rugosa</i>	<i>Clastoptera obtusa</i>	N. America	Hamilton, 1982
<i>Alnus serrulata</i>	<i>Clastoptera obtusa</i>	N. America	Mead & Bennett, 1987
<i>Alnus tenuifolia</i>	<i>Clastoptera obtusa</i>	N. America	Johnson & Lyon, 1991
<i>Alnus glutinosa</i>	<i>Aphrophora alni</i>	Europe	Ossiannilsson, 1981
<i>Alnus glutinosa</i>	<i>Aphrophora alni</i>	N. America (i)	Hamilton, 1982
<i>Myrica gale</i>	<i>Clastoptera saintcyri</i>	N. America (i)	Hamilton, 1982
<i>Comptonia peregrina</i>	<i>Aphrophora saratogensis</i> (n)	N. America (i)	Hamilton, 1982
<i>Ceanothus velutinus</i>	<i>Clastoptera ovata</i>	N. America (i)	Hamilton, 1982
<i>Ceanothus sanguineus</i>	<i>Clastoptera ovata</i> (a)	N. America (i)	Hamilton, 1982
<i>Casuarina stricta</i>	<i>Clastoptera undulata</i>	Bermuda (i)	Bennett & Hughes, 1963
<i>Casuarina stricta</i>	<i>Clastoptera undulata</i>	Florida (i)	Mead & Bennett, 1987
<i>Casuarina cunninghamia</i>	<i>Clastoptera undulata</i>	Bermuda (i)	Bennett & Hughes, 1963
<i>Casuarina cunninghamia</i>	<i>Clastoptera undulata</i>	Florida (i)	Mead & Bennett, 1987
<i>Casuarina cunninghamia</i>	<i>Clastoptera</i> sp.	Costa Rica (i)	Thompson (unpublished)
<i>Casuarina equisetifolia</i>	<i>Clastoptera undulata</i>	Bermuda (i)	Bennett & Hughes, 1963
<i>Casuarina equisetifolia</i>	<i>Clastoptera undulata</i>	Cuba (i)	Bennett & Hughes, 1963
<i>Casuarina equisetifolia</i>	<i>Clastoptera undulata</i>	Florida (i)	Mead & Bennett, 1987
<i>Casuarina glauca</i>	<i>Clastoptera undulata</i>	Florida (i)	Mead & Bennett, 1987
<i>Casuarina</i> sp.	<i>Clastoptera</i> sp.	Trinidad (i)	Williams, 1921
<i>Casuarina</i> sp.	<i>Clastoptera flavidorsa</i>	Jamaica (i)	Bennett & Hughes, 1963
<i>Casuarina</i> sp.	<i>Philigra parva</i>	Australia	Evans, 1966
? <i>Arctostaphylos uva-ursi</i>	<i>Clastoptera saintcyri</i> (a)	N. America	Hamilton, 1982
? <i>Arctostaphylos uva-ursi</i>	? <i>Aphrophora corticea</i> (n)	Europe	Ossiannilsson, 1981

Clastoptera and actinorhizal plants. *Clastoptera* have been recorded on 154 hosts: 144 angiosperms (all dicots), nine conifers and one fern (Thompson, unpublished review of hosts for about fifty species). At least ten of the angiosperm hosts are actinorhizal plants (Table 2). There are only 279 known actinorhizal species (Baker & Mullin, 1992), about 0.14% of the world angiosperm flora of 200,000 or so species. Were *Clastoptera* species distributed randomly over actinorhizal and non-actinorhizal hosts, we would expect less than one actinorhizal species in the *Clastoptera* host list. The probability of finding ten or more is less than 0.0001 (calculated using binomial probabilities with $n = 144$, $p = 0.9986$ and $q = 0.0014$), a highly significant association. *Clastoptera* are disproportionately attracted to actinorhizal plants.

Parallel analyses of cercopid and aphrophorid spittlebug host associations are impossible because comparable host lists are not available, and, more importantly, because most of these species are highly polyphagous. With polyphagy, the more thorough the host list, the cloudier preferences become, as more secondary and occasional hosts are included. However, analysis of spittlebug pests, most of them cercopids and aphrophorids, provides a third argument for association with nitrogen-fixing plants.

Table 1 lists thirty angiosperm species with well-documented spittlebug pests. Thirteen (44%) are known

nitrogen fixers. If 10% of all angiosperms are nitrogen-fixing (a very liberal estimate), then the probability that thirteen or more nitrogen fixers would occur by chance among thirty spittlebug pest hosts is less than 0.0001 (calculated using binomial probabilities with $n = 30$, $p = 0.9$ and $q = 0.1$). Moreover, the percentage of nitrogen fixers increases with the severity of the pest problem. They comprise 25%, 27% and 73%, respectively, of the host species suffering minor, medium and major spittlebug attack. It appears that nitrogen-fixing plants are disproportionately represented among plants with spittlebug pests and disproportionately susceptible to serious economic damage by spittlebugs.

This conclusion requires some caution. Whereas the number of nitrogen-fixing legumes and actinorhizal species is reasonably well known, the number of plant species with associative nitrogen-fixation is not. Only a dozen or so well-documented associative nitrogen-fixing species have been confirmed worldwide (Döbereiner & Pedrosa, 1987; Miranda & Boddey, 1987; Boddey & Döbereiner, 1988), no fewer than six of which have major spittlebug pests. This is an extraordinary coincidence. But the number of species rigorously tested for associative nitrogen fixation is small, the tests themselves are subject to major uncertainty, and there is considerable variation among strains of the same species. In the absence of reliable estimates of the

frequency of associative nitrogen fixers among cultivated species, statistical analysis can only be suggestive, not definitive.

Nitrogen-fixing plants are logical hosts for xylem feeders

There is a compelling physiological explanation for these spittlebug host preferences. Xylem sap is an energetically costly food source, consisting primarily of very dilute organic nitrogen compounds or inorganic nitrates, usually under negative pressure (Horsfield, 1977; Mattson, 1980; Raven, 1983). Xylem feeders must actively pump and process an enormous volume of fluid to obtain a modest residue of carbon compounds for growth and reproduction. Nitrogen-fixing plants transport fixed nitrogen in xylem sap as amino acids, amides and ureides (Sprent, 1980; Schubert, 1986). *P.spumarius*, the only spittlebug examined in this respect, seems to choose feeding sites based on amino acid concentration (Horsfield, 1977). It is likely, but unproven, that the xylem sap of nitrogen-fixing plants is relatively enriched and constant in organic nitrogen compounds, despite the paradoxical fact that these plants often occur in nitrogen-poor environments (Mattson, 1980). Spittlebugs, I suggest, favour nitrogen-fixing plants because they provide a relatively rich and reliable source of xylem-borne nutrients.

A variation on this hypothesis may explain the rarity of spittlebugs on certain legumes. Whereas the common polyphage *P.spumarius* achieves pest status on some legumes of the Tribe Trifoleae, such as *M.sativa* and *T.pratense*, it rarely occurs on legumes of the Tribe Phasoleae, such as *Glycine max* (L.) or *Phaseolus vulgaris* (L.). The Trifoleae transport fixed nitrogen as amino acids and amides while the Phasoleae transport fixed nitrogen as the ureides allantoin and allantoic acid (Sprent, 1980; Schubert, 1986). There is direct evidence that allantoin suppresses growth in bean beetles, and ureides may act as a general deterrent to insect attack (Wilson & Stinner, 1984). This may explain why spittlebugs are common on the actinorhizal nitrogen-fixers *Alnus* and *Casuarina* (Table 2) and tropical leguminous trees such as *Acacia* and *Erythrina*, which transport nitrogen as amino acids and amides (Schubert, 1986; Van Kessel *et al.*, 1988; Baker & Mullin, 1992), but rare on herbaceous tropical legumes, which usually transport nitrogen as ureides (Sprent, 1980; Schubert, 1986).

The association with nitrogen-fixing plants is not exclusive

Although host lists have been compiled for many spittlebugs of North America and Europe (Ossiannilsson, 1981; Hamilton, 1982), host plants for most species are unknown. Nevertheless, it is clear that the associations described here are far from exclusive. Many spittlebugs live on non-fixing host plants and many nitrogen-fixing plants are free from spittlebugs. Even among spittlebugs

that do feed on nitrogen-fixing hosts, alternative non-fixing hosts are the rule.

Ecological intolerance and mechanical or chemical defences may bar spittlebugs from feeding on some nitrogen-fixing plants. Wetland rice is ecologically unsuitable for spittlebug nymphs (Williams, 1918, 1921), an observation that may explain the scarcity of spittlebug pests of rice (Wilson & Claridge, 1991) despite the their occasional occurrence in Africa and Latin America (Table 1). Simple mechanical defences such as lignification or the presence of trichomes may bar some spittlebugs from other potential hosts (Hoffman & McEvoy, 1986). Such factors may explain the puzzling absence of *P.spumarius* on the common leguminous groundcover *Coronilla varia* (L.) (Wheeler, 1991, and personal observation) and its rarity on *Vicia cracca* (L.), an abundant and ostensibly desirable leguminous host in parts of Finland (Halkka *et al.*, 1967; Halkka & Halkka, 1990).

Whereas xylem sap is generally relatively free from chemical defences, some plants do have toxic xylem sap, and *P.spumarius* has not been reported on *Nicotiana*, a genus well defended by xylem-borne nicotine (Raven, 1983). Ureide nitrogen transport may also deter spittlebug attack (see above) but speculation concerning chemical defences is clouded by the long-standing observation that many insects, including at least two families and several genera of spittlebugs, exhibit an array of endosymbiotic micro-organisms (Buchner, 1965). These endosymbionts influence nitrogen metabolism (Buchner, 1965; Mattson, 1980) and could facilitate xylem feeding (Mattson, 1980) and ureide metabolism (Koch, 1967). To complicate matters, plants may use their own endosymbionts to ward off spittlebug attack. Plots of the pasture grass *Festuca arundinacea* (Schreb.) infected with a mutualistic fungal endophyte support 10-fold fewer *Prosapia bicincta* (Say) than uninfected plots (Muegge *et al.*, 1991). Given the diversity of nitrogen-fixing plants and the multiplicity of factors that determine insect host range, it is not surprising that spittlebugs are imperfect indicators of nitrogen fixation.

Discussion

Three lines of evidence converge to suggest that spittlebugs have an unusual affinity for nitrogen-fixing plants. First, there are statistically significant associations between spittlebugs and two groups of nitrogen-fixing host plants. Second, spittlebugs occur at high infestation levels on several introduced nitrogen-fixing hosts, suggesting that these hosts are intrinsically attractive to spittlebugs. Third, xylem feeding is physiologically consistent with attraction to nitrogen-fixing plants. Taken together, these facts suggest that the diversity and abundance of spittlebugs observed on nitrogen-fixing plants is not coincidental.

If spittlebugs have a preference for nitrogen-fixing hosts, they should serve as useful guides to undiscovered nitrogen-fixing plants. It is likely that many actinorhizal and associative nitrogen-fixing species remain to be found.

particularly in the tropics (Bond, 1983; Baker & Mullin, 1992). The recent detection of *Frankia* in Costa Rican habitats devoid of known actinorhizal plants (Paschke & Dawson, 1992) but full of spittlebugs (personal observation) suggests one area of promise. Investigators should seek nitrogen-fixing plants where spittlebugs abound.

Additionally, where nitrogen fixation varies with plant strain or ecological conditions, there should be corresponding variation in spittlebug attraction. Sugar cane, for example, exhibits marked varietal differences in associative nitrogen-fixing capacity (Döbereiner & Pedrosa, 1987; Urquiaga *et al.*, 1992). In Trinidad, blight caused by the spittlebug *Aeneolamia varia* (Fab.) often strikes hardest in cane fields with acidic, waterlogged soils (Carter, 1939). *Acetobacter diazotrophicus*, a bacterium associated with sugar cane roots, fixes nitrogen most effectively in acidic, low oxygen conditions (Stephan *et al.*, 1991). Some field-to-field variation in the severity of cane blight and other effects of spittlebug infestation may be due to variation in nitrogen fixation. This prediction is amenable to experimental verification. One could artificially manipulate nitrogen fixation levels among hosts and examine effects on spittlebug preferences.

Finally, spittlebugs are not the only xylem-feeding insects. Cicadas and the Cicadellinae, a leafhopper subfamily, also seem to be obligatory xylem feeders (Raven, 1983). The cicadelline leafhoppers are close ecological equivalents of spittlebugs. If spittlebugs show a special affinity for nitrogen-fixing plants, cicadelline leafhoppers might be expected to do the same. Whereas no comprehensive review of this group's host plants has been compiled, nutritional studies on two Florida cicadelline leafhoppers provide indirect corroboration for the ideas advanced above.

The leafhopper *Homalodisca coagulata* (Say) exhibits strong correlations between xylem amino acid concentrations and host plant preference, just as one would expect for a xylem feeder (Brodbeck *et al.*, 1990). More importantly, the key compounds that attract this leafhopper seem to be glutamine and asparagine, compounds conspicuous among the major xylem transport products in nitrogen-fixing plants known to attract spittlebugs (Sprent, 1980; Schubert, 1986; Baker & Mullin, 1992; and see above). A second Florida cicadelline leafhopper, *Carneiocephala floridana* (Ball), has been shown to prefer *Spartina alterniflora* host plants with higher nitrogen content (Rossi & Strong, 1991). This observation is particularly intriguing because *C. floridana* is a direct ecological analogue of the Canadian spittlebug *Philaenarcys spartina*. Both insects live in coastal salt marshes and both utilize the associative nitrogen-fixing grass *S. alterniflora* as a major host (Teal *et al.*, 1979; Hamilton, 1982; Rossi & Strong, 1991). The feeding ecology of cicadelline leafhoppers may provide a critical test of the thesis that xylem-feeding insects have a special attraction to nitrogen-fixing plants.

If this thesis holds up under scrutiny, there is more at stake than the recognition of a novel insect-plant interaction. Much research has been devoted to the artificial induction of nitrogen fixation in a variety of crop plants,

particularly grains. Artificial nitrogen fixation that mimics natural nitrogen fixation could make crops considerably more susceptible to spittlebug attack. The relatively rapid infestation of Old World nitrogen-fixing plants by New World spittlebugs suggests that this threat should be taken seriously and counter-measures actively explored before the widespread introduction of artificial nitrogen-fixing crops.

Acknowledgments

I thank J. A. Raven, J. I. Sprent, M. J. Hartman and anonymous reviewers for helpful comments on earlier versions of the manuscript. L. L. Deitz facilitated access to the Z. P. Metcalf Archives at North Carolina State University. F. Badilla (D.I.E.C.A.) and P. Hanson (University of Costa Rica) facilitated observations on Costa Rican sugar cane and *Casuarina* spittlebugs.

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Accepted 21 March 1994

Proposição para o manejo integrado das cigarrinhas-das-pastagens

J. R. Valério e W. W. Koller*

Introdução

As pastagens são culturas de baixo valor por unidade de área, isto favorece a adoção de táticas de manejo de pragas, uma vez que o pecuarista é um produtor acostumado a conviver com diferentes níveis populacionais de insetos em suas pastagens, diferentemente do agricultor tradicional que, devido ao maior valor por unidade de área de sua cultura, adota, muitas vezes, medidas preventivas de controle. Um outro aspecto que favorece a implementação do manejo de pragas em pastagens, é o fato de serem semi-perenes, permitindo a sua utilização por longo período de tempo. É importante considerar, no entanto, que a atividade na bovinocultura de corte no Brasil é basicamente extensiva, e que as práticas de manejo de pragas a serem recomendadas não poderão intensificar o sistema de produção. Deve-se pensar em medidas que sejam de baixo custo e fácil-adoção.

Caracterização do problema

A região do Cerrado vem sendo tradicionalmente ocupada pela bovinocultura de corte. Pelas características de solo fraco, esta região tem permitido uma utilização na base de uma unidade animal para cada 6-8 ha de pastagem nativa. No entanto, com a introdução de *Brachiaria decumbens*, a situação da pecuária de corte nesta região tem sido mudada. Esta gramínea

se adaptou às condições de baixa fertilidade e alta acidez dos solos dos Cerrados e hoje permite uma capacidade de suporte maior.

A aceitação por parte dos pecuaristas foi muito grande originando extensas monoculturas de *B. decumbens*. Infelizmente, nestas condições, esta forrageira permitiu explosões populacionais de insetos aos quais ela se mostrou altamente susceptível: o complexo cigarrinhas-das-pastagens (Homoptera: Cercopidae). Estes insetos são particularmente importantes devido a suas ocorrências generalizadas, aos altos níveis populacionais e a severidade dos danos que causam. Em função disso, estes insetos são considerados pragas chave para as pastagens de *B. decumbens*.

Em Brasil ocorrem diferentes espécies de cigarrinhas, devido a diversidades de ordem geográfica e climática, o programa de manejo não pode ser um único para todo o país.

O complexo das cigarrinhas-das-pastagens inclui as seguintes espécies, principalmente: *Deois incompleta* (Walker), na região norte do país; *Zulia entreriana* (Berg); *Deois schach* (F) e *Aeneolamia selecta* (Walker) importantes para o nordeste; e *Deois flavopicta* (Stål), que juntamente com *Z. entreriana*, predomina nos Estados do Brasil central, norte do Paraná e na região Leste.

A eclosão das ninfas das cigarrinhas, provenientes de ovos em diapausa, tem o seu início por ocasião do princípio da estação chuvosa, que no Brasil Central, por exemplo, acontece em setembro. Após a eclosão, as ninfas se alojam nas bases das touceiras, onde permanecem envoltas por uma massa espumosa, produzida pelas mesmas, até

* Pesquisadores, Centro Nacional de Pesquisa de Gado de Corte/ Empresa Brasileira de Pesquisa Agropecuária (CNPGC/ EMBRAPA), Rodovia BR 262, Km 4, Campo Grande, Mato Grosso do Sul, Brasil.

completarem o período ninfal, originando os adultos. Estes se acasalam, ocorre a oviposição e dão origem a uma nova geração. O ciclo ovo a ovo, varia com as diferentes espécies mas pode-se como base, dizer que o mesmo gira ao redor de 58 dias (incubação: 15 dias, período ninfal: 40 dias, e pré-oviposição: 3 dias). Atribui-se uma longevidade média de 10 dias às cigarrinhas adultas.

Considerações sobre as alternativas de controle

Inseticidas químicos. O uso de inseticidas químicos em pastagens depara-se com duas limitações importantes: a primeira, de ordem ecológica e, a segunda, de ordem econômica.

No caso particular de áreas destinadas à produção de sementes de gramíneas forrageiras, tais limitações são menores face a redução das áreas a serem tratadas e a maior margem de lucro desta atividade. Na maioria das vezes o produtor tem lançado mão desta ferramenta em ocasiões impróprias, motivado pela constatação de danos (amarelecimento das pastagens). Valério (1985) constatou que a sintomatologia dos danos causados por *Z. entriana* em *B. decumbens* se expressa plenamente após três semanas. Se considerarmos que a longevidade média destes adultos está ao redor de 10 dias, ao constataremos o pasto amarelecido, a quase totalidade da população responsável por aqueles danos, já teria morrido; não se justificando, portanto, a aplicação de inseticidas naquele momento.

Práticas culturais. Como mencionado anteriormente, no geral o sistema de exploração é extensivo e as proposições deverão se coadunar com tal realidade. As práticas culturais apresentam grande potencial neste aspecto. Todos concordam que o manejo da altura da gramínea pode contribuir no controle das cigarrinhas. Apesar de alguns pesquisadores entenderem que o pasto deva ser mantido alto, há ainda controvérsia a esse respeito. A queima das pastagens é prática tradicional e frequente. Esta medida, assim como a gradagem, efetuada por ocasião da renovação, são alternativas potencialmente úteis no controle das cigarrinhas.

Resistência de plantas aos insetos. Aqui reside a grande contribuição ao manejo de pragas de pastagens. A busca de alternativas,

se não para a substituição da *B. decumbens*, que sem dúvida será tarefa muito difícil, mas para a composição de um quadro mais diversificado no contexto de exploração, deve ser uma constante. Felizmente, estudos têm revelado algumas gramíneas com boas qualidades agronômicas que têm apresentado apreciável nível de resistência às cigarrinhas. Para efeito de uma correta diversificação é importante a inclusão de gramíneas de diferentes gêneros devendo-se inclusive, considerar a utilização, na medida do possível, de gramíneas nativas.

Controle biológico. Inimigos naturais das cigarrinhas têm sido reportados em vários trabalhos mas contesta-se sobre a abundância, variedade e eficiência dos mesmos. Este é sem dúvida, um campo que tem muito ainda a oferecer para o controle das cigarrinhas. A larva da mosca *Salpingogaster nigra* (Diptera: Syrphidae) tem sido um dos predadores mais citados atuando sobre ninfas de cigarrinhas, enquanto que o fungo entomógeno *Metarrhizium anisopliae* tem sido amplamente estudado, com potencial de se tornar arma importante no manejo destes insetos. No momento, no entanto, apesar dos inúmeros estudos, tem-se ainda observado inconsistência nos resultados de avaliações de controle através deste fungo.

Alguns resultados obtidos para fundamentar a proposição de manejo

Efeito de diferentes cargas-animais, durante o período seco do ano, nos níveis populacionais de cigarrinhas. Para muitas espécies de insetos, mudanças na planta hospedeira podem influenciar aspectos como sobrevivência, desenvolvimento, fecundidade, bem como a dispersão dos adultos (Kain et al., 1975). O manejo das pastagens, através da carga-animais, promove alterações nas plantas hospedeiras e se constitui numa ferramenta importante no controle de insetos de pastagens.

Os dados apresentados na Tabela 1 referem-se aos níveis populacionais de ninfas e adultos das cigarrinhas por ocasião do primeiro pico populacional. Este pico (primeira geração) é resultado dos níveis de infestação e de sobrevivência dos ovos em diáspora nas pastagens. Os levantamentos populacionais ocorreram ao longo de três anos, amostraram-se

Tabela 1. Nível populacional de cigarrinhas (*Zulia entreriana*), por ocasião do primeiro pico, em pastagens de *Brachiaria decumbens* cv. Basilisk submetidas a diferentes cargas-animal no período seco (maio-outubro). Média das infestações 1979-1980, 1980-1981 e 1981-1982.

Carga animal (UA/ha)*	Nível populacional	
	Ninfas/m ²	Adultos/m ²
1.0	100.9 a**	19.2 a
1.4	70.7 b	12.5 b
1.7	61.3 b	7.1 c

* Durante o período das águas (novembro a abril) a carga animal é única e igual a 2.5 UA/ha.

** Médias seguidas da mesma letra, dentro de cada coluna, não diferem entre si pelo teste de Tukey ($P < 0.05$).

ninfas e adultos em pastagens de *B. decumbens* que, no período da seca (maio a outubro) foram submetidas a três cargas-animal: 1.0, 1.4 e 1.7 unidades animal (UA/ha), e no período das águas (novembro a abril) permaneceram sob carga única de 2.5 UA/ha.

Aquí, a constatação mais importante deste trabalho refere-se ao fato de níveis populacionais mais elevados terem sido constatados nos pastos sujeitos a menor carga-animal, ou seja, nos pastos mais altos. Alguns trabalhos, mesmo que referindo-se a insetos diferentes, fundamentam esta observação. Dixon and Campbell (1978), afirmam que o aumento da carga-animal reduziu acentuadamente a população de *Costelytra zealandica* (Scarabaeidae) denominado "grass grub". Naito et al. (1977), verificando o efeito de cortes da pastagem na ocorrência de insetos e pragas, citam que a maioria dos insetos e aranhas diminuíram em número depois do corte. Observaram também que a abundância relativa de inimigos naturais e pragas aumentou com o corte e que, a habilidade predatória tendeu, algumas vezes, a aumentar na área cortada. Morris (1969), constatou diferenças entre a fauna de invertebrados em áreas pastejadas e não pastejadas. As populações aumentavam em muito seguindo-se o término do pasteio.

Efeito da remoção da cobertura vegetal morta (palha) em pastagens de *B. decumbens* sujeitas a diferentes cargas-animal. Ninfas e adultos foram amostrados semanalmente, ao longo de 17 meses, em parcelas onde se procedeu a remoção manual de palha (por meio de rastelos) e, em parcelas onde esta foi mantida. Verificou-se que o número médio de

ninfas por metro quadrado, e o de adultos por 10 redadas, foram menores ($P < 0.05$) nas parcelas em que a palha foi removida, independentemente da carga-animal à qual a pastagem esteve submetida (Tabela 2). As reduções médias para ninfas e adultos foram 60% e 30%, respectivamente. Hewitt (1986), observou maior sobrevivência dos ovos de cigarrinhas nas pastagens com mais de 30 cm de altura e que apresentavam abundância de palha em decomposição. Hewitt (1985), estudou a preferência de cigarrinhas quanto à oviposição, e verificou que a presença de palha foi sempre preferida para a postura, em comparação a um mesmo tipo de solo, com ausência de palha. Oomen (1975), afirma que os ovos em diapausa, encontram maiores possibilidades de sobrevivência sob uma camada de palha, onde conseguem proteção contra altas temperaturas. Seiffert (1978) relata que, ao se permitir sobras de forragem, os animais limitam-se a consumir as partes mais novas e tenras das plantas —particularmente verdadeiro para os meses de janeiro e fevereiro, no Brasil Central— permanecendo o restante intocado até a primavera seguinte, quando necessita ser removido, o que segundo Menezes et al. (1983) poderá ser feito através da queima ou roçagem, em benefício da rebroto da pastagem.

A sobra da forragem associa-se ao aumento do volume de palha acumulado no solo. Fagan (1969), afirma que pastagens com grande densidade de caules e touceiras, formam uma proteção contra ventos quentes (reduzindo à evaporação) e altas temperaturas, aumentando a taxa de sobrevivência de ninfas. Esse mesmo

Tabela 2. Efeito da remoção da palha em pastagens de *Brachiaria decumbens* submetidas a diferentes cargas-animal. Janeiro de 1983 a maio de 1984.

Carga-animal (UA/ha)*	Tratamento**	Ninfas (No./m ²)	Adultos (No./10 redadas)
1.0	SR	194.6 a***	106.6 a***
	CR	86.4 b	79.9 b
1.4	SR	36.9 a	19.2 a
	CR	12.1 b	12.2 b
1.7	SR	19.1 a	7.1 a
	CR	8.5 b	5.2 b

* Durante o período das águas (novembro a abril) a carga animal é única e igual a 2.5 UA/ha.

** SR = Sem remoção da palha; CR = com remoção da palha.

*** Médias seguidas da mesma letra, dentro de cada coluna e carga-animal, não diferem entre si pelo teste de Tukey ($P < 0.05$).

papel é desempenhado por plantas altas e, principalmente, pela palha acumulada ao nível do solo. Dessa forma, pastagens manejadas, dentro de certos limites, mais intensivamente resultam num menor acúmulo de palha e, conseqüentemente, expõe ovos e ninfas de cigarrinhas a um ambiente menos favorável à sua sobrevivência, produzindo, ao mesmo tempo, forragem de melhor qualidade para o consumo e o rendimento do rebanho.

Tratos culturais em pastagens e *Brachlaria decumbens*. A prática da limpeza das pastagens, através do fogo, é uma rotina em diversos estados brasileiros. Pastagens pouco produtivas ou em degradação também são, eventualmente, submetidas a gradagem e/ou outros tratos culturais visando o aumento de produtividade.

Parcelas de 1600 m² foram submetidas aos tratamentos queima e gradagem, após a primeira chuva de setembro, antes do aparecimento das primeiras ninfas. Constatou-se que ambos os tratamentos determinaram reduções significativas ($P < 0.05$) ao número de ovos (Tabela 3). A viabilidade dos ovos remanescentes também foi ($P < 0.05$) reduzida. Menezes e Pereira (1983), observaram que a temperatura durante a queima em pastagens chegou a 371 °C, matando as ninfas de cigarrinhas. Na combinação dos efeitos da queima e da gradagem, observou-se que a população de ninfas e adultos, até o quinto mês do período de infestação, foram menores ($P < 0.05$) em relação à testemunha (Tabela 4). A queima da pastagem geralmente não é necessária, desde que esta seja manejada de modo conveniente (Menezes et al., 1983). Já a

Tabela 3. Efeito da queima e da gradagem sobre o número e a viabilidade de ovos de cigarrinhas em pastagens de *Brachlaria decumbens*. Período de infestação 1985-1986.

Tratamento	Epoca das avaliações	Ovos coletados (No./m ²)	Viabilidade (%)	Ovos viáveis (No./m ²)
Gradagem	Antes	493 a*	89.41 a	441 a
	Depois	211 b	77.11 b	163 b
Queima	Antes	282 a	97.74 a	275 a
	Depois	242 b	8.95 b	22 b

* Os valores seguidos da mesma letra, dentro da cada coluna e tratamento, não diferem entre si, pelo teste de Tukey ($P < 0.05$).

Tabela 4. Efeito de tratos culturais executados em pastagens de *Brachlaria decumbens*, sobre as populações de cigarrinhas-das-pastagens. Período de infestação 1985-1986.

Tratamentos	Ninfas (No./m ²)		Adultos (No./10 redadas)	
	A*	B**	A*	B**
Testemunha	83.9 a	17.9 a	0.62 a	0.36 a
Queima + gradagem	0.2 b	2.3 b	0.07 b	0.11 b

* At o 70º dia do período de infestação.

** Do 70º ao 140º dia do período de infestação.

*** Os valores seguidos da mesma letra, dentro de cada coluna, não diferem entre si, pelo teste de Tukey ($P < 0.05$).

gradagem, poderá ser inevitável como meio de melhorar a produtividade de pastagens em degradação. Nesse caso, utilizar a queima antes da gradagem, facilita a execução desta e auxilia na destruição de maior número de ovos de cigarrinhas. Especificamente, em relação às cigarrinhas, no caso de áreas em que as mesmas sejam um problema grave e cíclico, práticas culturais como a queima e a gradagem, ou somente a queima, constituem armas potencialmente úteis para a minimização desse problema.

Seleção de gramíneas resistentes às cigarrinhas-das-pastagens. Nos estudos de resistência às cigarrinhas, entendemos que a objetivo principal deva ser a busca de gramíneas que apresentem como mecanismo de resistência a antibiose. Plantas com esta característica interfeririam no desenvolvimento, reduziram a sobrevivência, bem como o potencial reprodutivo das cigarrinhas. Como resultado teríamos uma redução nos níveis populacionais.

Avallaram-se o desenvolvimento e sobrevivência de ninfas da cigarrinha *Zulia entreciana* em diferentes gramíneas (*B. decumbens*, *B. humidicola*, *B. dictyoneura*, *B. ruziziensis*, *B. brizantha* e *Andropogon gayanus*) segundo metodologia proposta por Lapointe et al. (1989). Após o plantio das mudas, os vasos foram tampados (deixando-se uma abertura central para saída das plantas) com papel de alumínio. Tal procedimento visou, de um lado, estimular a emissão de raízes superficiais as quais são importantes para garantir a sobrevivência das ninfas recém-eclodidas, e de outro, prover um ambiente de menor aeração e luminosidade e maior umidade às ninfas. Após

dois meses e meio do plantio, as plantas foram infestadas com 15 ovos prestes a eclodirem. Identificaram-se dois grupos distintos:

(1) *Brachiaria humidicola*, *B. ruziziensis*, *B. decumbens*, *B. dictyoneura* incluindo gramíneas que propiciaram maior taxa de sobrevivência, e (2) *B. brizantha* e *A. gayanus*, onde se verificou o oposto. Nenhuma ninfa completou o desenvolvimento em *A. gayanus*, e um número muito reduzido o fez em *B. brizantha*. Observou-se que aquelas que propiciaram maior sobrevivência foram justamente aquelas nas quais o desenvolvimento se processou mais rapidamente. Isto caracteriza tais gramíneas como plantas adequadas ao desenvolvimento das cigarrinhas, diferentemente da *B. brizantha* e *A. gayanus*. Verificou-se para o caso da *B. brizantha* que o período ninfal se estendeu por um período de quase uma semana além da média das demais gramíneas.

Testes como este, permitem identificar material apresentando antibiose às cigarrinhas. No caso, *B. brizantha* e *A. gayanus* tem sido reportados como resistentes em outros trabalhos (Nilakhe, 1987; Cosenza et al., 1989). Estas duas gramíneas constituem atualmente nas melhores alternativas para um programa de manejo para as cigarrinhas em pastagens.

E oportuno fazer aqui, referência à *B. humidicola* que na realidade, é resistente às cigarrinhas através do mecanismo tolerância. Esta gramínea tem-se revelado boa hospedeira para estes insetos favorecendo a multiplicação dos mesmos, ou seja, contribuindo para o aumento dos níveis populacionais.

As considerações feitas neste item, ilustram o potencial de linha de pesquisa no controle destes insetos. Com as avaliações hoje em fundamento, envolvendo germoplasmas do gênero *Brachiaria* (aproximadamente 800 introduções) e de *Panicum maximum* (em torno de 400 introduções) espera-se encontrar outras gramíneas resistentes que permitirão a composição de sistemas mais diversificados de exploração.

Proposição para o manejo integrado das cigarrinhas das pastagens

Quanto maior o conhecimento sobre o problema, maior a chance que se propor um bom programa

de manejo. O conhecimento atual sobre as cigarrinhas-das-pastagens ainda é pequeno. Por exemplo, não dispomos de informações básicas como o nível de dano econômico. No entanto, mesmo na ausência desta e outras informações, deve-se tentar implementar um programa de manejo baseando-se no bom senso, conhecimentos e experiências atuais. Isto significa dizer que, trata-se de um processo dinâmico e que portanto, à luz de novos conhecimentos, possíveis alterações poderão se feitas no manejo até então proposto. O enfoque principal deste conjunto de medidas reside na tentativa de se evitar que as populações de cigarrinhas atinjam proporções epidêmicas, ao invés de se tentar controlar populações em níveis epidêmicos. Oferece-se algumas medidas que mesmo isoladamente contribuem para a redução de níveis populacionais das cigarrinhas. A implementação destas medidas, em parte ou no todo, dependerá da necessidade e características da propriedade e possibilidades do produtor. São elas:

- (1) Diversificar as pastagens a nível de propriedade com a inclusão de gramíneas resistentes as cigarrinhas.

Sugere-se, *Brachiaria brizantha* cv. Marandú e *Andropogon gayanus* cv. Planaltina, e evitar o estabelecimento de áreas extensas com um único tipo de gramínea, procurando intercalar áreas de gramíneas susceptíveis com gramíneas resistentes.

- (2) Manejar as pastagens, adequando a carga-animal, de modo a evitar sobra de pasto. Esta prática deverá ser implementada em caráter permanente, principalmente nos meses do ano quando ocorre pico de produção de forragem. No Brasil Central, por exemplo, estes meses são janeiro e fevereiro. A sobra de pasto, que venha ocorrer nestes meses, originará material vegetal morto que contribuirá para o acúmulo de palha ao nível do solo.

As cigarrinhas, nas condições de Brasil central, concentram a oviposição de ovos em diapausa principalmente entre os meses de março a maio (Koller et al., 1989). Estes ovos permanecem nas pastagens até a eclosão das ninfas no início da época das chuvas. É de grande importância que durante este período, as condições sejam adversas à sobrevivência destes ovos.

Em atingindo o objetivo —pastagens com reduzida quantidade de palha ao nível do solo—, o produtor poderá aliviar a pressão de pastejo por ocasião de março-abril, permitindo um aumento na produção de forragem visando a alimentação do gado no período seco. Aquí os animais poderão ser anejados em áreas tradicionalmente menos sujeitas a altas infestações bem como, para pastagens estabelecidas com gramíneas resistentes.

- (3) Queima controlada, podendo estar associada à gradagem, em áreas com histórico de altas infestações após as primeiras chuvas. Sugere-se adotar a queima controlada, nas áreas que tradicionalmente apresentam altas infestações. Esta medida, se bem conduzida será particularmente útil na eliminação de grande parte da palha acumulada até então, facilitando a adoção da tática de manejo proposta no item anterior. A queima em associação com gradagem, principalmente nas áreas de pastagens a serem reformadas, ou mesmo nas áreas que têm apresentado níveis populacionais extremamente altos.
- (4) Uso de inseticidas. Como mencionado anteriormente, a utilização de inseticidas químicos no controle das cigarrinhas em pastagens se depara com aspectos de ordem ecológica e econômica. Embora não se tenha avaliado neste trabalho imposição visa fornecer subsídios àqueles que optarem por esta medida de controle.

Inicialmente, é importante lembrar o aspecto sobre a adoção do controle químico em ocasiões inadequadas. O pasto queimado pelas cigarrinhas indica que os danos já ocorreram e que a maior parte da população, responsável por estes danos, já morreu. Desta forma, o produtor deverá monitorar os níveis populacionais de ninfas através de observações no campo. Muito embora não se tenha definido ainda o nível de dano econômico para estes insetos, através de resultados preliminares acredita-se que o controle deva ser implementado após a constatação de uma população entre 20 a 25 ninfas grandes (tamanho semelhante ao do adulto) por metro quadrado. O produto deverá ser aplicado quando da emergência da maior parte dos adultos. Como no campo existem ninfas de diferentes idades, poderá

ser necessária a reaplicação do produto após um intervalo de uma semana.

Resumen

Se presentan algunos resultados y se discute el empleo de insecticidas, de prácticas culturales, de plantas resistentes y del control biológico en el manejo integrado de cercópidos (*Deois incompleta*, *Zulia entreriana*, *D. schach*, *D. flavopicta* y *Aeneolamia selecta*) en pasturas de *Brachiaria*. Con base en estas experiencias se hacen varias propuestas para el manejo de esta plaga.

Summary

Some results and discussion are presented on the use of insecticides, cultural practices, resistant plants, and biological control in the integrated management of cercopidae (*Deois incompleta*, *Zulia entreriana*, *D. schach*, *D. flavopicta*, and *Aeneolamia selecta*) in *Brachiaria* pastures. Based on these experiences, several proposals are made for the management of this pest.

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DANOS CAUSADOS PELO ADULTO DA CIGARRINHA *ZULIA ENTRERIANA* NA PRODUÇÃO E QUALIDADE DE *BRACHIARIA DECUMBENS*¹

JOSÉ RAUL VALÉRIO² e OCTAVIO NAKANO³

RESUMO - Os danos causados pelas cigarrinhas reduzindo a capacidade de suporte das pastagens, são de grande importância em vários países centro e sul-americanos. Visando a obtenção de alguns elementos, que pudessem contribuir na tomada de decisão quanto ao controle desses insetos, desenvolveu-se o presente trabalho, onde se procurou avaliar os danos causados pelo adulto da cigarrinha *Zulia entreriana* (Berg 1879) (Homoptera: Cercopidae), na produção e qualidade de *Brachiaria decumbens* Stapf cv. Basilisk. Estabeleceram-se quatro níveis populacionais (zero, 25, 50 e 100 adultos por metro quadrado) utilizando-se gaiolas. As plantas no interior destas, tiveram suas alturas padronizadas em 25 cm. As infestações foram mantidas por dez dias. Após esse período procederam-se os cortes para as avaliações de produção e qualidade. Constataram-se reduções significativas ($P < 0,05$) na produção. Vinte e cinco adultos por metro quadrado reduziram, em 30%, a produção de matéria seca de *B. decumbens*. Sobre a qualidade desta forrageira, estes insetos diminuíram, significativamente ($P < 0,05$), os teores de proteína bruta, fósforo, cálcio, magnésio e potássio, e aumentaram ($P < 0,05$) os teores de matéria seca e de fibra.

Termos para indexação: pastagem, nível de dano, insetos, Homoptera, Cercopidae.

DAMAGE CAUSED BY THE PASTURE SPITTLEBUG *ZULIA ENTRERIANA* ON PRODUCTION AND QUALITY OF *BRACHIARIA DECUMBENS*

ABSTRACT - Damage caused by spittlebugs reducing pasture stocking densities, is of great importance in several Central and South-American countries. The present work was conducted, in order to obtain further elements which could be useful in developing strategies for the control of such insects. The objective was to evaluate damage caused by the adult of *Zulia entreriana* (Berg 1879) (Homoptera: Cercopidae) in the production and quality of *Brachiaria decumbens* Stapf. cv. Basilisk. Four population densities were evaluated (zero, 25, 50 and 100 adults/square meter) with the use of cages. Plants within these cages were cut at a standard height of 25 cm. Infestations were maintained for ten days. After this period, evaluations for production and quality were undertaken. Significant reductions ($P < 0,05$) in production were observed. The density of 25 adults/m² reduced by 30% dry matter production of *B. decumbens*. In relation to forage quality, the insects reduced significantly ($P < 0,05$), levels of crude protein, phosphorous, calcium, magnesium and potassium, and increased ($P < 0,05$) dry matter and fiber contents.

Index terms: insect damage, loss assessment, grass, Homoptera, Cercopidae.

INTRODUÇÃO

Os danos causados pelas cigarrinhas-das-pastagens são reconhecidamente importantes em vários países centro e sul-americanos. Quando em altas populações, estes insetos reduzem acentuadamente a capacidade de suporte das pastagens. Objetivando o controle das cigarrinhas, inúmeros trabalhos têm sido realizados enfocando aspectos básicos como biologia (Ramos 1976), taxonomia (Sakakibara

1979), dinâmica populacional (Milanez 1980) e de plantas hospedeiras (Menezes 1982). No que tange ao controle propriamente dito, deu-se ênfase, a princípio, ao controle químico (Puzzi et al. 1962). Mais recentemente, métodos alternativos como o controle biológico (Barbosa et al. 1984) e o controle cultural (Ramiro et al. 1984) têm sido avaliados.

No entanto, apesar da vasta literatura disponível a respeito destes insetos, são raros os trabalhos que tratam mais diretamente da avaliação dos danos causados pelas cigarrinhas.

A avaliação dos danos causados por insetos em pastagens é uma tarefa difícil. São inúmeros os fatores a serem considerados e que levaram Kain & Atkinson (1975) a concluir que a determinação precisa dos níveis de dano para insetos-praga em pastagens é praticamente impossível. Aqueles autores afirmam que o principal problema, associa-

¹ Aceito para publicação em 7 de janeiro de 1987. Parte da Tese do primeiro autor para obtenção do título de Doutor em Ciências (Entomologia) junto à ESALQ/USP.

² Eng. - Agr., Dr., EMBRAPA/Centro Nacional de Pesquisa de Gado de Corte (CNPGC), Caixa Postal 154, CEP 79001 Campo Grande, MS.

³ Eng. - Agr., Dr., Dep. de Entomol., ESALQ/USP, Caixa postal 9, CEP 13400 Piracicaba, SP.

do aos estudos que avaliam os danos de insetos em pastagens, é a conversão das perdas quantitativas e qualitativas das pastagens em produção animal. Concordam que esta conversão é necessária para que os danos sejam adequadamente avaliados, mas estabelecem como um dos principais objetivos a serem atingidos, a previsão de níveis populacionais e seus danos resultantes.

Segundo Stern (1973), uma das primeiras etapas na determinação de níveis de dano, é justamente o conhecimento do relacionamento entre densidade populacional e a produção e/ou qualidade. Pedigo (1972) afirma que a avaliação dos danos causados por insetos se constitui num dos aspectos mais importantes no estabelecimento de estratégias de controle. Sem o entendimento do relacionamento entre número de insetos e produção, não há fundamentação nas recomendações de controle.

Assim sendo, procurou-se com o estabelecimento de diferentes níveis populacionais de adultos da cigarrinha *Zulia entreariana*, avaliar os danos causados por estes insetos, na produção e qualidade de *Brachiaria decumbens*.

MATERIAL E MÉTODOS

Neste experimento, utilizaram-se 36 gaiolas (1.0 m x 1.0 m x 0.6 m), que foram identificadas e distribuídas em pontos aparentemente homogêneos de uma pastagem de *B. decumbens*. Em seguida, as plantas no interior de cada gaiola tiveram suas alturas padronizadas em 25 cm. A porção cortada do interior de cada gaiola foi individualizada em saco de plástico e encaminhada ao laboratório para obtenção do peso verde. Com isso, procurou-se confirmar a homogeneidade dos locais da pastagem, escolhidos para a colocação das gaiolas.

Uma vez que se constatou razoável variação entre os pontos escolhidos, optou-se por agrupar os valores obtidos, de sorte que o delineamento experimental usado foi um ensaio em blocos ao acaso. Os tratamentos, com nove repetições, representando diferentes níveis populacionais, foram os seguintes: zero, 25, 50 e 100 adultos de *Z. entreariana* por metro quadrado. Ao longo do período experimental, que correspondeu à longevidade média destes insetos, ou seja, dez dias, as cigarrinhas, na sua totalidade, foram substituídas diariamente. Procurou-se com isso, manter os níveis populacionais nos diversos tratamentos o mais constante possível.

Inicialmente, logo pela manhã, procurava-se retirar as cigarrinhas remanescentes do interior das gaiolas com o uso de redes entomológicas, para imediatamente após, repor o número de cigarrinhas do tratamento corresponden-

te. Esta foi uma operação que, em média, levava uma hora e meia para ser efetuada.

Além das 36 gaiolas que compuseram o ensaio, outras três, também ocupando uma área de um metro quadrado cada, foram utilizadas. Diferentemente das demais, estas tinham altura de 1,2 m e um tampo removível para permitir a entrada de uma pessoa. Aqui, procurou-se acompanhar a mortalidade diária nos três tratamentos com cigarrinhas. Portanto, uma dessas gaiolas recebeu 25 cigarrinhas, a outra 50, e a terceira 100. Diariamente, antecedendo as substituições das cigarrinhas, uma pessoa entrava no interior dessas gaiolas e cuidadosamente, com um aspirador, procurava capturar todas as cigarrinhas vivas e remanescentes da infestação feita no dia anterior. Com esses dados pode-se conhecer os percentuais diários de mortalidade nos diversos tratamentos.

Findo o período de dez dias de infestação, os insetos foram retirados e as gaiolas mantidas nos respectivos locais. Aplicou-se Diclorvos (NUVAN(R) 100) (1 ml/l) no interior dessas gaiolas para evitar reinfestação e após cinco dias, prazo dado para que a sintomatologia se expressasse ainda mais, tiveram início as observações.

Após as anotações das alturas nos diversos tratamentos, foram feitos os cortes das parcelas da seguinte maneira: a) rebrote, toda porção das plantas que cresceu acima da altura de padronização (25 cm), feita no início do teste; b) base, porção das plantas desde o nível do solo até a altura de 25 cm.

De posse dos pesos verdes dessas porções, este material foi submetido à secagem, em estufas (65°C, 48 horas), para obtenção do peso seco e também do teor de matéria seca (peso seco/peso verde).

Para efeito de análises bromatológicas e de minerais (teores de proteína bruta, fibra em detergente neutro, fósforo, cálcio, magnésio e potássio), além das informações pertinentes às porções-base e rebrote individualmente, reservou-se 25% da área de cada parcela que tiveram suas porções (base e rebrote) reunidas num só conjunto. Isto permitiu que se obtivessem dados dessas análises, não apenas sobre porções (base e rebrote) de plantas, mas também, dados referentes às plantas como um todo.

As técnicas utilizadas para a determinação destes parâmetros qualitativos foram: Harris (1970), para proteína bruta; Soest (1967), para fibra em detergente neutro; e Tedesco (1982), para minerais.

Ao longo do período experimental, a temperatura média foi de 24,6°C e a umidade relativa de 79,3%, obtidos de um posto meteorológico localizado a 100 m da área experimental.

As médias foram comparadas estatisticamente pelo teste de Tukey utilizando-se o nível de 5% de probabilidade.

RESULTADOS E DISCUSSÃO

Na Tabela 1 são apresentados os dados referentes ao efeito dos diferentes níveis populacionais

de adultos de *Zulia entreriana*, sobre a altura e produção de matéria seca de *Brachiaria decumbens*, em condições de campo. Todos os tratamentos reduziram significativamente a altura da gramínea em relação à testemunha. Os tratamentos 25, 50 e 100 cigarrinhas por metro quadrado, reduziram a altura das plantas em aproximadamente, 25%, 35% e 45%, respectivamente. Considerando a altura de uniformização de 25 cm, estabelecida no início do teste, estes níveis populacionais reduziram o crescimento de *B. decumbens* em relação à testemunha em, aproximadamente, 50%, 65% e 80%, respectivamente. Estes dados mostram claramente o quanto estes insetos restringem o desenvolvimento dessa forrageira. Silva (1982), avaliando os danos causados pela cigarrinha *Deois incompleta* em *B. decumbens*, verificou, para o nível populacional de 40 adultos por metro quadrado, uma redução no crescimento dessa gramínea ao redor de 65%.

Os dados referentes às variações verificadas nas produções de matéria seca dos rebrotes nos vários tratamentos, sem dúvida, revestem-se de grande importância no presente trabalho. Na realidade, correspondem aos efeitos que seriam observados numa pastagem de *B. decumbens*, com altura de 25 cm, quando submetida a estas infestações durante dez dias. Pelos dados da Tabela 1, observa-se que 25 cigarrinhas por metro quadrado reduziram significativamente a produção de matéria seca do rebrote em relação à testemunha. Esta redução

foi da ordem de 30%. Os demais níveis populacionais, 50 e 100 cigarrinhas por metro quadrado, reduziram a produção de matéria seca do rebrote em relação à testemunha em 50% e 65%, respectivamente.

Cem cigarrinhas por metro quadrado determinaram uma redução na produção de matéria seca do rebrote, não muito superior àquela verificada para o tratamento com 50 adultos. Isto talvez pudesse sugerir uma maior taxa de mortalidade naquele tratamento, face à grande densidade de insetos; no entanto, dados dos três tratamentos obtidos diariamente, revelaram níveis de mortalidade semelhantes. Para os tratamentos, 25, 50 e 100 cigarrinhas por metro quadrado, as taxas médias de mortalidade foram 24,0%; 28,2% e 26,6%, respectivamente.

Para uma infestação de 40 adultos de *Deois incompleta*, mantida por 48 dias, Silva (1982) verificou uma redução de 25% na quantidade de forragem de *B. decumbens* disponível. Dados do Centro Internacional de Agricultura Tropical (1982), envolvendo a cigarrinha *Zulia colombiana* e *B. decumbens*, mostram uma redução de 83,7% na produção de forragem, para uma infestação de 39 cigarrinhas por 1,25 metro quadrado (aproximadamente 30 cigarrinhas por metro quadrado). Não há neste trabalho, menção sobre a duração da infestação.

Duzentos adultos da cigarrinha *Aeneolamia va-*

TABELA 1. Efeito de diferentes níveis populacionais de adultos de *Zulia entreriana* (Berg 1879) mantidos por dez dias, na altura e produção de matéria seca de *Brachiaria decumbens* cv. Basilisk. Campo Grande, MS, 1985.

Número de adultos/m ²	Altura (cm)	Peso seco (g/m ²) - rebrote ¹		Peso seco (g/m ²) - base ²	
		Dados originais	Dados transformados ³	Dados originais	Dados transformados ³
0	54,6 a ⁴	66,5	8,07 a ⁴	297,8	17,24 a ⁴
25	40,1 b	44,1	6,58 b	255,0	16,00 ab
50	35,0 c	33,7	5,75 bc	259,6	16,09 ab
100	31,1 d	23,9	4,91 c	246,1	15,66 b
CV (%)	5,6		16,6		7,3
DMS	2,9		1,3		1,5

¹ Refere-se ao crescimento da forrageira verificado acima da altura de uniformização (25 cm) feita no início do teste.

² Refere-se à porção das plantas compreendida entre o nível do solo e a altura de 25 cm.

³ Dados transformados para $\sqrt{x + 0,5}$.

⁴ Médias seguidas da mesma letra não diferem entre si pelo teste de Tukey, ao nível de 5% de probabilidade.

ria em dois metros quadrados de pasto de *B. decumbens*, mantidos por 32 dias, curiosamente não determinaram reduções significativas na produção desta gramínea, num trabalho realizado na Colômbia, por Jimenez (1978). Ochoa & Velasco (1971), verificaram que 50 adultos de *Aneolamia postica* por metro quadrado, em pastos de *Cynodon maritimus* e *Cynodon plectostachyus*, reduziram a produção de matéria seca em, aproximadamente, 34% e 42%, respectivamente.

Reportando-se aos dados obtidos no presente trabalho, considerando-se apenas os efeitos causados pela infestação de 25 cigarrinhas por metro quadrado, e consciente das limitações associadas a qualquer tipo de extrapolação, tem-se que, na ausência das cigarrinhas, a produção de matéria seca de uma pastagem de *B. decumbens* com 25 cm de altura, em um hectare, durante dez dias, seria de 665 kg.

Um bovino adulto (450 kg de peso vivo = uma unidade animal, UA) consome em média 10 kg de matéria seca por dia (Empresa Brasileira de Pesquisa Agropecuária 1984). De posse desta informação, pastagens de *B. decumbens* nas condições do experimento e na ausência de cigarrinhas, permitiriam uma capacidade de suporte de 6,65 UA/ha, durante dez dias, contra uma capacidade de suporte de 4,41 UA/ha, que seria verificada em virtude da infestação de 25 adultos de *Z. enteriana* por metro quadrado.

Dados obtidos por Seiffert (1984) mostraram um ganho de peso por animal por dia de 0,890 kg. O autor refere-se a animais com peso inicial entre 350 kg e 400 kg, mantidos durante a estação chuvosa, em pastagem de *B. decumbens* estabelecida num solo Latossolo Roxo Álico, textura argilosa, fase cerrado, que não recebeu adubação e que apresentou um pH médio de 4,7, fósforo = 1 ppm a 4 ppm e potássio = 30 ppm a 50 ppm. Baseando-se neste ganho diário de 0,890 kg por animal, para as condições do experimento, a ausência de cigarrinhas permitiria ao longo de dez dias, a produção de, aproximadamente, 59 kg de carne, contra apenas 39 kg que seriam obtidos no mesmo período, em pastagens de *B. decumbens* sujeitas à infestação de 25 adultos de *Z. enteriana* por metro quadrado. Esta diferença poderia ser ainda maior, considerando-se que os pastos com sinto-

mas de danos causados pelas cigarrinhas, são referidos como menos palatáveis.

É sabido que a produção de matéria seca de *B. decumbens* e a capacidade de suporte das pastagens, são parâmetros que sofrem variações estacionais. Mesmo dentro da estação chuvosa, a taxa de crescimento da forragem é variável, e por conseguinte, a capacidade de suporte média de pastagens de *B. decumbens* ao longo do ano é bem inferior àquelas mencionadas anteriormente. Por isso, a extrapolação feita é válida apenas para as condições e para o período de duração do experimento.

A produção de matéria seca da porção basal das plantas de *B. decumbens* mostrou-se menos sensível aos diferentes níveis de infestação estudados. Redução significativa em relação à testemunha, foi observada apenas no tratamento 100 cigarrinhas por metro quadrado (Tabela 1).

Variações impostas a alguns parâmetros qualitativos da *B. decumbens*, resultantes da ação dos diferentes níveis populacionais estudados, são apresentadas nas Tabelas 2 e 3. Não se constataram diferenças significativas quanto a estes parâmetros no que se refere à base e à planta como um todo.

Os dados apresentados, a seguir, referem-se apenas ao rebrote. No geral, em função da sucção imposta pelas cigarrinhas, constatou-se um aumento no teor de matéria seca nas plantas de *B. decumbens* com o aumento do nível populacional. Diferenças significativas em relação à testemunha, no entanto, foram verificadas apenas nos tratamentos mais altos, ou seja, 50 e 100 cigarrinhas por metro quadrado.

Weaver & Hibbs (1952) e Marthur & Pienkowski (1967), trabalhando com *Philaenus spumarius* em alfafa e trevo vermelho, e Fagan (1969), trabalhando com *Prosapia bicincta* em *Digitaria decumbens*, constataram, à semelhança do verificado no presente trabalho, um aumento no teor de matéria seca nestas plantas hospedeiras em razão dos danos impostos pelas cigarrinhas.

Os níveis populacionais estudados, exceção feita à infestação de 25 cigarrinhas por metro quadrado, determinaram reduções significativas nos teores de proteína bruta em *B. decumbens*. As reduções observadas nos tratamentos 50 e 100 cigarrinhas por metro quadrado, foram semelhantes e ao

TABELA 2. Efeito de diferentes níveis populacionais de adultos de *Zulia entreriana* (Berg 1879), mantidos por dez dias nos teores de matéria seca, proteína bruta e fibra em detergente neutro, do rebrote¹ de *Brachiaria decumbens* cv. Basilisk. Campo Grande, MS, 1985.

Número de adultos por m ²	Matéria seca (%)		Proteína bruta (%)		Fibra em detergente neutro (%)	
	Dados originais	Dados transformados ²	Dados originais	Dados transformados ³	Dados originais	Dados transformados ²
0	30,5	33,11 a ⁴	10,3	3,28 a ⁴	69,5	53,16 a ⁴
25	34,8	35,67 ab	8,3	2,97 ab	74,4	55,36 ab
50	39,7	38,38 b	7,2	2,75 b	78,5	57,21 bc
100	38,8	38,00 b	6,7	2,68 b	80,8	58,24 c
CV (%)		6,3		9,5		3,6
DMS		2,9		0,4		2,6

¹ Refere-se ao crescimento da forrageira verificado acima da altura de uniformização (25 cm) feita no início do teste.

² Dados transformados para arco seno de $\sqrt{x/100}$.

³ Dados transformados para $\sqrt{x} + 0,5$.

⁴ Médias seguidas da mesma letra não diferem entre si, pelo teste de Tukey, ao nível de 5% de probabilidade.

TABELA 3. Efeito de diferentes níveis populacionais de adultos de *Zulia entreriana* (Berg 1879), mantidos por dez dias, nos teores de fósforo, magnésio, cálcio e potássio do rebrote¹ de *Brachiaria decumbens* cv. Basilisk. Campo Grande, MS, 1985.

Número de adultos por m ²	Fósforo (%)		Magnésio (%)		Cálcio (%)		Potássio (%)	
	Dados originais	Dados transformados ²	Dados originais	Dados transformados ²	Dados originais	Dados transformados ²	Dados originais	Dados transformados ²
0	0,23	0,856 a ³	0,20	0,839 a ³	0,27	0,875 a ³	2,7	1,778 a ³
25	0,23	0,856 a	0,18	0,827 ab	0,25	0,866 ab	2,4	1,696 b
50	0,20	0,835 ab	0,17	0,817 b	0,23	0,854 ab	2,3	1,661 b
100	0,19	0,831 b	0,15	0,809 b	0,21	0,844 b	2,3	1,661 b
CV (%)		2,1		1,8		2,2		3,3
DMS		0,023		0,019		0,025		0,073

¹ Refere-se ao crescimento da forrageira verificado acima da altura de uniformização (25 cm) feita no início do teste.

² Dados transformados para $\sqrt{x} + 0,5$.

³ Médias seguidas da mesma letra não diferem entre si, pelo teste de Tukey, ao nível de 5% de probabilidade.

redor de 30%.

Segundo Seiffert (1984), para que haja um crescimento satisfatório em ruminantes, o teor de proteína bruta deve estar acima de 7%. Observando-se os dados de proteína bruta, obtidos nos presente trabalho (Tabela 2), apesar das significativas reduções constatadas em alguns tratamentos, os teores obtidos, mesmo no nível populacional mais alto, atendem a esta exigência nutricional em bovinos. Isto sugere que apenas nos casos de infestação extremamente altas, é que a redução nos teores de proteína nas pastagens de *B. decumbens* deve merecer maior atenção.

Os dados apresentados na Tabela 2, revelam que o aumento nos níveis populacionais de adultos de *Z. entreriana* determinou aumentos significativos

nos teores de fibra. Isto é uma clara indicação da remoção dos conteúdos celulares pelos adultos desta cigarrinha.

Complementando as avaliações dos danos causados pelo adulto de *Z. entreriana* na qualidade de *B. decumbens*, a Tabela 3 apresenta os efeitos dos diferentes níveis populacionais estudados nos teores de fósforo, magnésio, cálcio e potássio, no rebrote desta forrageira. Os dados obtidos revelam que estas cigarrinhas, dependendo do nível populacional, determinam reduções significativas nos teores destes minerais. Particularmente para cálcio e fósforo, a redução significativa só foi observada para a infestação de 100 cigarrinhas por metro quadrado.

Segundo dados da Empresa Brasileira de Pesqui-

sa Agropecuária (1984), o fósforo, que é um elemento mineral importante na nutrição animal, é deficiente nos bovinos em quase todo o território nacional. A ação da cigarrinha *Z. entreciana*, mesmo que apenas em níveis populacionais mais elevados, contribui para acentuar esta deficiência.

Quanto ao cálcio, segundo esta mesma fonte, sua deficiência em bovinos em pastejo é pouco frequente. Talvez, a redução imposta pela cigarrinha no teor deste mineral, em plantas de *B. decumbens*, não se revista de maior importância.

Magnésio é outro elemento mineral sobre o qual não se tem, segundo Empresa Brasileira de Pesquisa Agropecuária (1984), registros de deficiências em plantas forrageiras nas condições brasileiras. Admite-se que a deficiência de magnésio seja mais comum em países de clima temperado. A redução no teor de magnésio verificada no presente trabalho, se não tão importante, pode ser o reflexo da destruição da clorofila causada pelas cigarrinhas. Como se sabe o magnésio é parte integrante deste pigmento.

Quanto ao potássio, que segundo Empresa Brasileira de Pesquisa Agropecuária (1984), é o elemento mineral de maior concentração nas forrageiras, observaram-se reduções significativas nos seus teores já a partir do nível populacional mais baixo, ou seja, 25 adultos por metro quadrado.

Weaver & Hibbs (1952), sobre a ação de *P. spumarius* na qualidade da alfafa e trevo vermelho, afirmam que as análises químicas indicaram diferenças no teor de proteína, mas que não foram suficientes para se poder afirmar que as cigarrinhas reduzem o valor nutricional do feno obtido daquelas culturas.

Washbon (1968) verificou grande redução nos teores de proteína e cinza mineral em *Stenotaphrum secundatum*, resultante da ação da cigarrinha *Prosapia bicincta*.

Dados do Centro Internacional de Agricultura Tropical (1984), referentes aos efeitos do adulto de *Zulia colombiana* na qualidade de forrageiras do gênero *Brachiaria*, atestam que aparentemente a concentração de nutrientes das plantas não é influenciada pelo dano causado por esta cigarrinha.

Os resultados obtidos no presente trabalho sobre a ação do adulto da cigarrinha *Z. entreciana* na qualidade de *B. decumbens*, como pode ser obser-

vaço pelo que foi exposto anteriormente, indicaram diferenças significativas em todos os parâmetros avaliados. No entanto, a real importância destas diferenças, principalmente sob o ponto de vista de nutrição animal, e em face das considerações que foram feitas, é desconhecida, merecendo, portanto, considerações por parte de especialistas em nutrição animal.

CONCLUSÃO

A alimentação imposta pelo adulto da cigarrinha *Zulia entreciana* reduz o crescimento e a produção de matéria seca de *Brachiaria decumbens*, bem como a qualidade desta forrageira, reduzindo os teores de proteína bruta, fósforo, magnésio, cálcio e potássio e aumentando os teores de matéria seca e fibra.

AGRADECIMENTOS

Os autores são gratos a Wilson Werner Koller, Marlene Conceição Monteiro Oliveira, Lélia Inês Z. Vera, Gustavo O. Paschoale e Valdomiro Marques Correa, a colaboração prestada na condução deste experimento.

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SINTOMATOLOGIA DOS DANOS CAUSADOS PELO ADULTO DA CIGARRINHA
Zulla entreriana (BERG, 1879) (HOMOPTERA, CERCOPIDAE) EM
Brachiaria decumbens STAPF¹

José R. Valério² • Octávio Nakano³.

ABSTRACT

Symptoms of *Zulla entreriana* (Berg, 1879) (Homoptera, Cercopidae) damage in *Brachiaria decumbens* Stapf plants

A direct relationship between length of feeding and extension of symptoms was observed. Confining the insect for only one hour was enough to detect symptoms, both on leaves and stems of *Brachiaria decumbens* Stapf.

On the leaves, mainly in those treatments where the insects were confined longer (2, 4 and 8 days), the necrotic lesions spread longitudinally toward the leaf apex far from the feeding site. The same was observed when feeding occurred on the stems. In some cases the symptoms were observed on the basal portion of the first and second leaves above the feeding site.

For both leaves and stems, the full expression of symptoms took about three weeks. Considering that the adult lives for about 10 days, this information is particularly important as to the timing of insecticide application, which should not be done when the pastures are browned off, since most of the adults responsible for that damage, had already died.

Recebido em 6/11/90

¹ Parte de tese apresentada à ESALQ-USP, para obtenção do título de Doutor em Ciências, Área de Entomologia.

² EMBRAPA-Centro Nacional de Pesquisa de Gado de Corte (CNPGC), Caixa Postal 154, 79001 Campo Grande MS, Brasil.

³ Departamento de Entomologia, Escola Superior de Agricultura "Luiz de Queiroz", Caixa Postal 9, 13400 Piracicaba SP, Brasil.

RESUMO

Observou-se uma relação direta entre tempo de alimentação e intensidade de sintomas. O período mínimo de uma hora de confinamento foi suficiente para o aparecimento de sintomas.

Quando o confinamento do inseto se deu nas folhas, particularmente para os períodos de 2, 4 e 8 dias, as áreas necrosadas estenderam-se muito além do local de alimentação. As várias folhas que secaram totalmente (períodos de alimentação mais longos), em geral começaram a secar a partir do ápice, adquirindo aspecto retorcido.

No caule, a dinâmica dos sintomas foi semelhante àquela verificada nas folhas. Nos períodos de alimentação mais longos, houve casos em que os sintomas foram constatados não só na base da primeira folha, mas também na base da segunda folha acima do local de confinamento.

Tanto nas folhas como nos colmos, os sintomas manifestaram-se em sua plenitude após três semanas. Este fato é particularmente importante quando da decisão de se controlar quimicamente as cigarrinhas, uma vez que a longevidade média dos adultos é de apenas 10 dias e que, a decisão de se controlar tem sido, na maioria das vezes, motivada pelo amarelecimento das pastagens.

INTRODUÇÃO

Os prejuízos causados pela cigarrinha *Zulia entreriana* (Berg, 1879), reduzindo a capacidade de suporte das pastagens, são reconhecidamente importantes em inúmeros estados brasileiros.

Os principais danos são atribuídos aos adultos das cigarrinhas, que, ao se alimentarem, injetam secreções salivares fitotóxicas (BYERS & WELLS, 1966).

O objetivo do presente trabalho foi o de acompanhar a progressão dos sintomas de danos ocasionados por adultos de *Z. entreriana*, em função do local e tempo de alimentação, em plantas de *Brachiaria decumbens* Stapf.

MATERIAL E MÉTODOS

O experimento foi conduzido em casa telada, na área experimental do Centro Nacional de Pesquisa de Gado de Corte (CNPGC) da Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), em Campo Grande, MS.

Adultos de *Z. entreriana*, independentemente de sexo ou idade, foram confinados em partes específicas das plantas de *B. decumbens* por tempo variável. Este confinamento deu-se através do uso de seções de um tubo plástico flexível e transparente (3,0 cm x 1,5 cm de diâmetro). Por esta seção de tubo, introduzia-se a folha até que o mesmo se situasse nas partes desejadas. No presente trabalho, estas partes foram: a) folha na sua porção mediana e face superior e b) bainha da folha, incluindo o talo, também na sua porção mediana. As extremidades destas pequenas gaiolas foram fechadas, confinando a cigarrinha no seu interior, usando-se dois pedaços de espuma de látex. A fim de se evitar que as folhas dobrassem devido ao peso dessa pequena gaiola, um barbante foi amarrado à mesma, de sorte a suspender a e permitir que a folha permanecesse em sua posição normal. Externamente estas gaiolas foram identificadas de acordo com os respectivos tratamentos que se constituíram em diferentes períodos de confinamento para aquelas duas regiões da planta, e foram os seguintes: 1, 2, 4 e 8 horas; e 1, 2, 4 e 8 dias. Houve dez repetições para cada tratamento. Sempre que necessário, as cigarrinhas mortas foram substituídas prontamente ao longo do teste.

Em função do número de tratamentos e repetições, utilizaram-se dez vasos com plantas de *B. decumbens* apresentando altura aproximada de 35 cm. Estes vasos foram espalhados sobre balcões no interior de uma casa telada.

Ao término do período correspondente a cada tratamento, as cigarrinhas foram retiradas, permanecendo, entretanto, as pequenas gaiolas para identificação dos locais de alimentação correspondentes. Desta forma, as folhas foram mantidas nas plantas e esperou-se um período de 30 dias para que a sintomatologia, em cada tratamento, se expressasse na sua plenitude.

O acompanhamento da evolução dos sintomas foi diário, e após o período experimental, as folhas foram removidas e montadas em herbário. Durante o período máximo de confinamento das cigarrinhas (8 dias), a temperatura média foi de 22,9°C e a umidade relativa de 68.1%; já para o período de 30 dias subsequente, a temperatura média foi de 22,9°C e a umidade relativa de 74,0%.

RESULTADOS E DISCUSSÃO

Observou-se claramente uma relação direta entre tempo de exposição e intensidade dos sintomas. BYERS & WELLS (1966) obtiveram resultados semelhantes em estudos desenvolvidos com *Protopia bicincta* em capim-bermuda. Neste estudo, os autores confinaram adultos desta cigarrinha por períodos que variaram desde uma hora até sete dias. Concluíram que a severidade dos danos foi diretamente proporcional ao tempo em que o inseto ficou confinado junto à planta.

No presente trabalho, constatou-se variabilidade entre as repetições, a qual decresceu com o aumento do tempo de alimentação. Assim sendo, para o tempo de uma hora, apenas duas das

dez folhas estudadas mostraram sintomas de danos. Isto está de acordo, no entanto, com as observações de BYERS & WELLS (1966), de que o período mínimo de uma hora é suficiente para o desenvolvimento de sintomas.

Os primeiros sinais de danos foram vistos no terceiro dia após o início da alimentação do inseto. Para o período de uma hora, uma pequena área clorótica foi observada ao redor do ponto de sucção. Esta área se estendia num raio de aproximadamente 3 mm. Este quadro progrediu paulatinamente, adquirindo sua expressão plena e definitiva após 23 dias. Nesta ocasião, muito embora os sintomas de danos fossem leves, estes eram generalizados no sentido longitudinal (apenas na metade longitudinal da folha onde a alimentação se processou), atingindo uma área de aproximadamente 10 cm de comprimento por 0,8 cm de largura. Algumas estrias cloróticas foram observadas, expandindo-se no sentido apical, indo além do limite desta área de sintomas mais visíveis.

A medida em que se aumentou o tempo de alimentação, observou-se não só um aumento na área apresentando sintomas, como também um aumento na intensidade dos mesmos. Para os tempos de alimentação mais curtos, de uma hora até um dia, estas áreas necrosadas eram restritas e localizadas ao redor dos locais de alimentação. Margeando estas áreas necrosadas, haviam áreas de acentuada clorose cuja intensidade diminuía à medida que se afastava do local de alimentação. Para os períodos de alimentação de 2, 4 e 8 dias, estas áreas necrosadas estenderam-se muito além do local de alimentação e com muito mais intensidade. As várias folhas que secaram, particularmente nos tratamentos de períodos de alimentação mais longos, começaram, de modo geral, a secar a partir do ápice. Segundo WITTHYCOMBE (1926), a clorose das folhas estende-se na direção longitudinal, mas principalmente no sentido do ápice. Este autor também notou que a porção apical das folhas secava mais rapidamente do que a porção basal. Isto se deve em parte, segundo este autor, provavelmente ao maior suprimento de água que deve ocorrer na posição basal da folha, uma vez que ficou constatado no seu trabalho um número de nervuras transversais maior na base do que na porção apical da folha.

Após 19 dias do início da alimentação, no tratamento de 8 dias, houve folhas cujas porções apicais, além de estarem necrosadas, apresentaram-se retorcidas. Neste tratamento, assim como mencionado anteriormente, houve variações quanto à expressão dos sintomas. Muito embora sete das dez folhas apresentassem áreas necrosadas que representaram 80 a 100 por cento da área foliar, três folhas apresentaram sintomas bem aquém do esperado, e que poderiam perfeitamente se confundir com sintomas verificados nos tratamentos 3 horas e 1 dia. Acredita-se que seja uma variação associada mais às plantas do que aos insetos, uma vez que estes foram substituídos em algumas oportunidades ao longo dos 8 dias, face às mortes que invariavelmente ocorreram. Talvez a idade da folha, seu nível de lignificação, por exemplo, explique essa menor expressão dos sintomas.

A semelhança do que foi feito para folhas, promoveu-se o confinamento de adultos de *Z. entreriana* também no colmo (inclu-

indo aqui a bainha da folha) de *B. decumbens*. Como verificado em trabalho anterior (VALÉRIO & NAKANO, 1988), as cigarrinhas, em 20% dos casos, alimentam-se nesta região da planta. O interesse foi, então, conhecer a expressão dos sintomas nestes locais. Aqui também, da mesma forma verificada para as folhas, a expressão dos sintomas foi proporcional ao período de alimentação. Os danos foram observados não só no local de alimentação, mas também nas bases das folhas, imediatamente acima destes locais. Em alguns casos, particularmente nos períodos de alimentação mais longos, os sintomas de danos foram mais além, atingiram as bases da primeira e também da segunda folha acima dos locais de alimentação. BYERS & WELLS (1966) verificaram que o confinamento de um adulto de *P. bicincta* na porção mediana do colmo (bainha de folha removida) do capim-bermuda, resultou em sintomas nas folhas, tanto acima como abaixo do local de alimentação. Estes autores verificaram também que, quando a alimentação era feita acima da bifurcação do colmo, os sintomas apareciam nas folhas acima e abaixo do local de confinamento, mas não no braço ramificado do colmo.

Confirmou-se uma vez mais, neste teste, que apenas uma hora de alimentação resulta em sintomas de danos. Os primeiros sinais de dano apareceram também no terceiro dia após o confinamento do inseto. Tratava-se de um pequeno ponto amarelado. Progressivamente, uma clorose se difundia ao redor deste ponto, de forma que no sexto dia após o confinamento, na base da metade longitudinal da folha, correspondente ao ponto de sucção, observou-se uma faixa clorótica com dimensões aproximadas de 0,5 cm de largura por 1 cm de comprimento. Estes sintomas manifestaram-se plenamente após 22 dias. No colmo, observou-se uma necrose generalizada a partir do local de confinamento no sentido apical, e na base da folha uma faixa levemente clorótica se estendendo apicalmente, atingindo 6 cm de comprimento por 0,8 cm de largura, apresentando algumas estrias cloróticas alcançando até 10 cm. O período de alimentação de 8 horas determinou, em pelo menos um caso, áreas necrosadas, ainda que restritas, tanto no colmo como na margem da folha, na sua porção basal.

No período de confinamento mais longo, ou seja, oito dias, os danos foram maiores tanto na extensão como na intensidade. Em vários casos os sintomas estenderam-se até a segunda folha acima do local de alimentação. Quando a primeira e a segunda folha estavam bem próximas e, portanto, ocorria a sobreposição das bainhas das mesmas, o aparecimento de sintomas na segunda folha era mais facilmente entendido. Numa das repetições em que as folhas estavam mais afastadas, e onde não ocorria a sobreposição das bainhas, o aparecimento de sintomas na segunda folha sugere uma alimentação no próprio colmo, como foi verificado também por BYERS & WELLS (1966).

Em um dos casos, onde os sintomas surgiram apenas na primeira folha acima do local de alimentação, observaram-se áreas com necroses generalizadas, tanto no talo como na folha. Os tecidos na base da folha morreram, talvez indicando que a ação das toxinas injetadas pelo adulto de *Z. entrerianu* se verificou apicalmente, mas apenas até o terço basal da folha. A morte que

foi verificada nas porções mediana e apical desta folha, pode ser explicada pela não translocação da seiva, em decorrência da degeneração dos tecidos na base das folhas.

Cumpramos ressaltar novamente, que, tanto nas folhas como nos colmos, a expressão plena dos sintomas de danos deu-se após três semanas. Isto é particularmente importante, se considerarmos a longevidade dos adultos das cigarrinhas. Com base nos trabalhos de alguns (DOMINGUES & SANTOS, 1975; RAMOS, 1976; JIMENEZ, 1980; MAGALHÃES & SILVA, 1980; ARANGO & CALDERON, 1981 e FERNANDEZ & RAMOS, 1986) conclui-se que a longevidade média das cigarrinhas está ao redor de dez dias. Portanto, admite-se que, em muitos casos, a decisão de se controlar quimicamente estes insetos, com base na constatação de danos, tem resultado em aplicações em ocasião inadequada. Nesta ocasião a maior parte da população de adultos, responsável por aqueles danos, já teria morrido há algum tempo.

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Cercopid spittle as a microhabitat

J. B. WHITTAKER

Department of Biological Sciences, University of Lancaster

Whittaker, J. B. 1970. Cercopid spittle as a microhabitat. - *Oikos* 21: 59-64. Copenhagen.

Some observations and experiments are described which support the generally accepted view that «cuckoo-spit» has the function of protecting cercopid nymphs from desiccation, natural enemies and also from high temperatures. Although the nymphs do not control the quantity of spittle produced, evaporation rate gradients ensure that spittles are largest near the ground surface where nymphs are likely to be most easily available to non-flying predators, and where a greater insulation from high temperatures is required.

Dr. J. B. Whittaker, Dept. of Biological sciences, St. Leonard's House, St. Leonardgate, Lancaster, England.

Описаны некоторые наблюдения и эксперименты, подтверждающие общепринятое мнение, что функцией слюны *Cercopidae* является защита нимф от высыхания, от естественных врагов и высокой температуры. Нимфы не регулируют количество выделяемой слюны. Однако, в результате неравномерного испарения, наибольшее количество слюны оказывается вблизи поверхности почвы, где нимфы могут скорее всего стать добычей летающих хищников и где требуется защита от высоких температур.

1. Introduction

The presence of foam or spittle on many plants in spring and early summer has attracted the attention of naturalists for centuries. Theories ranging from its production by the cuckoo (*Cuculus canorus* L.) (attributed to St. Isidore of Seville), to the natural exudation of the plants themselves (Bock, 16th Century) or when punctured by Homoptera (Fabre 1900), have been accepted until recent times. It was, however, pointed out by Blankaart as early as 1690 that the fluid came from the anus of the insect which lives within the spittle, and the mechanism of its production by nymphs of the homopterous family Cercopidae has now been described by such authors as Sule (1911), Gahan (1918) and Cecil (1930). It is now considered that the liquid is an anal exudate of similar composition to the juices of the host plant, but containing less sugar and amino-acids because these have been utilised for nutriment (Wilson and Dorsey 1958). This liquid appears at the anus shortly after the insect begins to feed. When the nymph becomes partially submerged, bubbles are blown into the liquid from a canal formed by extensions of the abdominal tergites. These form an enclosed space under the abdomen into which air is drawn from outside the spittle. This air is then blown into the liquid and the bubbles so formed are stabilised by a substance secreted by the abdominal glands.

There are 10 species of spittle-producing Cercopidae in Britain and these, with one exception, produce spittle on the aerial parts of plants, though in some species (e.g. *Neophilaenus eximius* (Thun.) and *Neocenturus* (Fall.) it may be very close to the ground surface and only observed with difficulty. *Aphrophora ulmi* (Fall.) when found in shaded woodland herbage produces very conspicuous spittles often up to several feet from the ground surface, but in open grassland the nymphs are restricted to the base of the herbs so that although quite common in such habitats, they are rarely seen. Here they may frequently feed on a plant which also has *Philaenus spumarius* (L.) spittles on it, but the latter are usually much higher on the plant. *Cercopis vulnerata* Illiger is the only British species with truly subterranean spittle masses.

Protection from predators or parasites and from unfavourable microclimatic conditions are two of the functions attributed to the spittle by various authors (e.g. Buckton 1890). Neither appear to have been examined critically and the survival value of the spittle has not been demonstrated. This account is of some simple experiments and observations which examine the function of the spittle masses produced by nymphal Cercopidae in Britain.

2. Protection from predators and parasites

The foam will serve as protection from predators only if they do not associate its presence with that of the nymph. If such an association occurs, the foam will be a

disadvantage because it is much more easily seen than the nymph itself. There are several references to birds having been observed to take nymphs from spittles (e.g. Kalmbach 1919, 1940, Brindley 1934, Nolan 1956, Macklin 1958), but with one exception, these are records of isolated incidents. Brindley quotes Fincher who had observed house sparrows *Passer domesticus* (L.) which "deliberately pecked them (*Philaenus spumarius* nymphs) out of the cuckoo-spit and took a good beakful on each occasion". Royama (pers. comm. and in Lack 1968) has shown that great tits (*Parus major* L.) feed their young to some extent on *Aphrophora* nymphs and that they may constitute an important part of the bird's diet for short periods. This agrees with the observations of Haines (1942) who recorded that several species of tits fed on *Aphrophora* sp. nymphs infesting *Salix caprea* L. at the end of June. By the beginning of July hardly any *Aphrophora* remained, implying that the birds had decimated them. However, this is just about the time when adult *Aphrophora* would be emerging from the spittles and so the decline in spittle numbers could at least be in part associated with this event. Spittles of *Philaenus spumarius* lower down in the herbage were not noticeably reduced by the birds. There is even less evidence of predation on nymphs from spittle by invertebrates although Westwood (1840) describes *Gorytes mystaceus* L. (Hymenoptera) dragging a nymph from its spittle and Imms (1960) says that "they are not infrequently seized from their spume by fossorial Hymenoptera and other enemies". A study of the fate of radioactively labelled cercopid nymphs (Brumpton pers. comm.) has not provided any evidence of systematic predation by invertebrates.

In spite of the records cited, there is little evidence of frequent predation of cercopid nymphs by vertebrates or invertebrates. Two experiments were carried out to study the effect of predation on spittles of *Philaenus spumarius* and *Neophilaenus lineatus* (L.).

Eight 0.25 m² wire bird enclosures were erected over spittles of the two cercopid species on an area of open grassland at Upper Seeds, Wytham Woods, Berkshire (described by Elton 1966). Eight similar frames, but with open tops allowing bird access, were erected as controls. The two kinds of frame were positioned randomly and the numbers of nymphs in each frame were recorded. The nymphs were re-counted after 15 and 30 days had elapsed. The results are given in Tab. 1a. There is a possibility that the presence of open frames as controls would affect the behaviour of birds. They were, however, used in this experiment in order to prevent the entrance of non-flying predators through the sides of the frame. In a repeat of the experiment at the University of Lancaster field station the control area had no frames at all. The result is given in Table 1b. There is no evidence from these experiments that cercopid nymphs protected from birds had a significantly

Tab. 1. The survival of *P. spumarius* and *N. lineatus* nymphs when exposed to bird predation and when birds are excluded.

a) At Wytham Woods.					
Date	Exlosures Survivors		Controls Survivors		χ^2
	Number	%	Number	%	
13.5	219	100	227	100	
28.5	141	64	127	56	3.03, $p > 0.05$
11.6	113	52	112	49	0.23, $p > 0.05$
b) At Lancaster University Field Station.					
Date	Exlosures Survivors		Controls Survivors		χ^2
	Number	%	Number	%	
27.6	43	100	38	100	
7.7	28	65	26	69	0.11, $p > 0.05$

higher survival rate than those exposed to bird predation.

A second experiment on the Wytham Woods study area was an attempt to determine to what extent the presence of spittle around a nymph protected it from predation. This cannot be done directly because nymphs removed from spittle will usually rapidly produce more, or will not survive long for reasons other than predation. In this experiment, 20 freshly killed nymphs of *N. lineatus* were placed in marked, occupied spittles so that the occupant kept the dead nymphs surrounded by spittle. Thirty similar nymphs were exposed in small trays (kept humid) in the vegetation. The disappearance of the nymphs was recorded over a 48 hour period (Tab. 2).

Tab. 2. Removal by predators or scavengers of cercopid nymphs when surrounded by spittle or when exposed.

	Dead nymphs surrounded by spittle	Dead nymphs exposed in the vegetation
No. established.....	20	30
No. remaining after 48 hours.....	14 ¹	8
% disappearance.....	30	73
¹ See note in text.		

Although this is a highly artificial experiment because the nymphs were not alive, it does indicate that dead nymphs without surrounding spittle are significantly more likely to be found and carried away by other animals than are those in spittle ($\chi^2 = 4.2$ $p < 0.05$). The six nymphs which were lost after being surrounded by spittle were almost certainly not dragged from the spittle, but were exposed as a result of the spittle drying up. Loss actually from spittles was therefore probably nil.

Nymphs of those Homoptera Auchenorrhyncha which are unprotected by spittle (Cicadellidae and Delphacidae) are commonly parasitised by Dryinidae (Hymenoptera), Strepsiptera or Pipunculidae (Diptera). Although there are one or two known cases of a cercopid having a parasite in the nymphal stage (e.g. a dryinid attacking *Thomaspis* (Williams 1921) and an encyrtid attacking *Clastoptera* (Myers 1930)), there are no records in the literature of parasitism of nymphal Cercopidae in Britain, and Whittaker (1969) has shown that although Pipunculidae (Diptera) do attack cercopids, the genus of pipunculid concerned is unique in attacking adults rather than nymphs.

3. Contents of spittle

Wilson and Dorsey (1958) have shown that spittle masses are a favourable environment for many species of bacteria. Myers (1930) suggested that larval Drosophilidae (Diptera) may be inquilines in the spittle of *Clastoptera* and Odhiambo (1958) bred *Leucopheuga* (Drosophilidae) from spittle masses of *Pyelus*. They also act as natural traps for small invertebrates which come into contact with them. Thus out of 30 randomly chosen instar four and five spittles of *N. lineatus* at 1800 ft (549 m) in the Pennine Hills, 17 spittles contained a total of 32 invertebrates (mainly Diptera and Hymenoptera). A survey of these inquilines was made at Upper Seeds grassland, Wytham Woods in 1964. The results are given in Tab. 3. In most cases it is not known whether the animals were alive or dead at the time of collection.

Two facts emerge from this survey. Firstly there are significantly more inquilines in the *N. lineatus* spittles than in the *P. spumarius* spittles ($\chi^2 = 4.3$; $p < 0.05$) though the latter spittles are at least as big as the former. Secondly, the groups of invertebrates differ in the two situations. (For Diptera, Acari and "the rest", $\chi^2 = 16.9$; $p < 0.001$). The mites particularly are quite common in

Tab. 3. Invertebrates found in spittle masses of *N. lineatus* and *P. spumarius*.

	<i>N. lineatus</i> spittles	<i>P. spumarius</i> spittles	Total
No. spittles examined	944	440	1384
No. containing invertebrates other than Cercopidae...	112	34	146
Invertebrates:			
Psychodidae.....	30	1	31
Other Diptera.....	13	6	19
Acari.....	29	0	29
Collembola.....	23	8	31
Hymenoptera.....	10	7	17
Thysanoptera.....	12	4	16
Araneida.....	2	1	3
Homoptera - other than cercopids...	5	5	10
Lepidoptera.....	0	2	2
Total invertebrates...	124	34	158

N. lineatus spittles but are absent in *P. spumarius* spittles; whilst the difference in the Diptera is due mainly to the presence of 30 Psychodidae in the *N. lineatus* spittles and only one in the *P. spumarius* spittles. These differences probably reflect the fact that *N. lineatus* spittles tend to be much nearer the ground surface than *P. spumarius* spittle. It is not known whether any of these inquilines actually use the spittle (e.g. as a larval habitat) rather than be trapped in it accidentally.

4. The microclimate of cercopid nymphs

Many invertebrates are unable to survive in conditions of low humidity so that they are restricted to moist environments. For insects feeding on the succulent aerial parts of plants, such restrictions would mean that feeding could perhaps only take place intermittently when suitable points in microclimatic gradients corresponded with acceptable food sources. Cercopidae, however, actively produce their own microclimate and it has been shown (Weaver and King 1954) that newly hatched nymphs die rapidly if unable to produce spittle. Studies of this unusual microclimate were carried out in the laboratory and in the field.

4.1. Laboratory experiments

Spittle is a by-product of feeding and so it may be expected that the nymphs will be unable to control the size of their spittle to any great extent. It is much more likely that the size of a spittle will depend on the time spent at that site on the plant by a nymph of a given instar, and the rate of evaporation of the spittle. This was tested experimentally in the laboratory (20 °C), using nymphs of *N. lineatus* feeding on grass. A portion of cut turf was placed on a gauze in a desiccator containing water up to the level of the gauze. This was sealed until a high humidity (saturation) was established, and then 5 final instar nymphs were introduced at various heights in the vegetation in each of three such containers. To ensure that the nymphs would feed at the positions at which they were placed on the plants, the desiccator was covered to exclude light. (In daylight, nymphs placed on a plant will move down towards the base of the plant before commencing feeding. In darkness, however, they do not move much before feeding.) A similar series of experiments was set up in which the desiccators contained a little water in the base, but calcium chloride was placed above the vegetation. This had the effect of producing a gradient of humidity ranging from saturation at the water surface to 14 mb S.D. above the vegetation. Five final instar nymphs were introduced into each of three such desiccators.

After 10 hours, the resulting spittle sizes (expressed as maximum spittle width) and their heights in the vegetation were recorded (Fig. 1). Not all the nymphs successfully produced spittle.

In the vegetation which had no humidity gradient (Fig. 1A) the size of the spittle was not correlated with

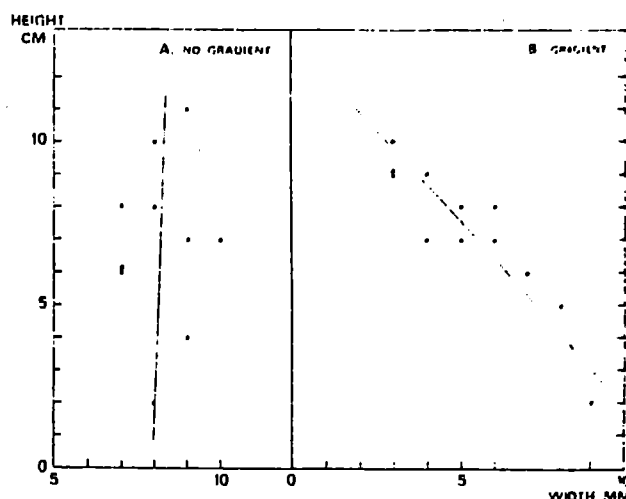


Fig. 1. The relationship between spittle width and its height on the host plant in experimental laboratory cultures. a) In a saturated atmosphere ($y = 7.96 + 0.035x$). b) In a humidity gradient of 35–100 per cent R.H. ($y = 11.7 - 0.89x$).

its height on the plant ($r = +0.08$, 8 d.f.). That is to say, whether or not the nymphs were feeding near to the base of the plant or high on the leaves or stems, the spittle production was the same, presumably because food intake was similar. In a steep humidity gradient (Fig. 1B), however, spittles near to the base of the plants (in a humid atmosphere) were larger than those high on the plants (which were presumably evaporating much more rapidly). There was thus a high negative correlation between spittle height and spittle size ($r = -0.95$, 10 d.f.).

Rates of evaporation were also compared in an experiment in which spittles of equal volumes from which the nymphs had been removed, were placed (on a portion of their host plant) in a dry atmosphere (S.D. 19 mb) or in a saturated atmosphere. Those in the dry atmosphere were all completely evaporated within 4 hours whilst those in the saturated atmosphere persisted for 30 hours (when the experiment was concluded).

4.2. Field observations

Temperature gradients in the field were recorded by measuring resistance changes occurring in thermistors as a result of temperature changes. Humidity gradients were measured by using two temperature probes mounted parallel to each other and about 1.5 cm apart with single threads of white (to minimise the effects of direct radiation) cotton wrapped several times around the constricted neck of both beads. In several tests with one thread moistened with water from a pipette this device gave results within 2% R.H. of those obtained with an aspirated Assmann psychrometer. Temperatures within the spittles were recorded with very fine thermistors coated with several layers of shellac to insulate the lead wires and prevent shorting.

The relationship of spittle size to its height from the ground was examined in a field close to the Science Laboratories of Durham University and on an area of *Juncus squarrosus* L. at the Moor House National Nature Reserve, Westmorland.

In the lowland field, 30 spittles of *N. lineatus* showed a negative correlation of size and height ($r = -0.78$), and this was also the case on the *Juncus* area at much higher altitude (for 40 spittles, $r = -0.88$). The data are reproduced in Figs. 2 and 3. It can be seen that the rate of change of spittle size with height is much greater at the high altitude site where pronounced wind speed gradients will presumably lead to a very steep evaporation gradient (e.g. Fig. 4). These rather simple relationships between spittle height and spittle size in grassland must no doubt be obscured in more complex vegetation stands such as *Philaenus spumarius* may inhabit. Here

the complicated growth forms of herbs may produce humidity gradients which are partially independent of the height from the ground surface.

A fairly typical humidity gradient in a stand of *Nardus stricta* L. on which *N. lineatus* nymphs were feeding is shown in Fig. 4B. Fig. 4A shows that the air temperature displays a typical incoming radiation-type gradient so that spittles close to the ground surface may be exposed to higher temperatures than those in the upper part of the vegetation. The question arises as to whether the greater quantity of spittle surrounding nymphs near to the ground will act as a more efficient insulator so that the relatively immobile nymphs may be protected from high temperatures developing near to the ground during day-time incoming radiation. Whilst the temperature and humidity gradients shown in Fig. 4 were being recorded, thermistor probes were inserted

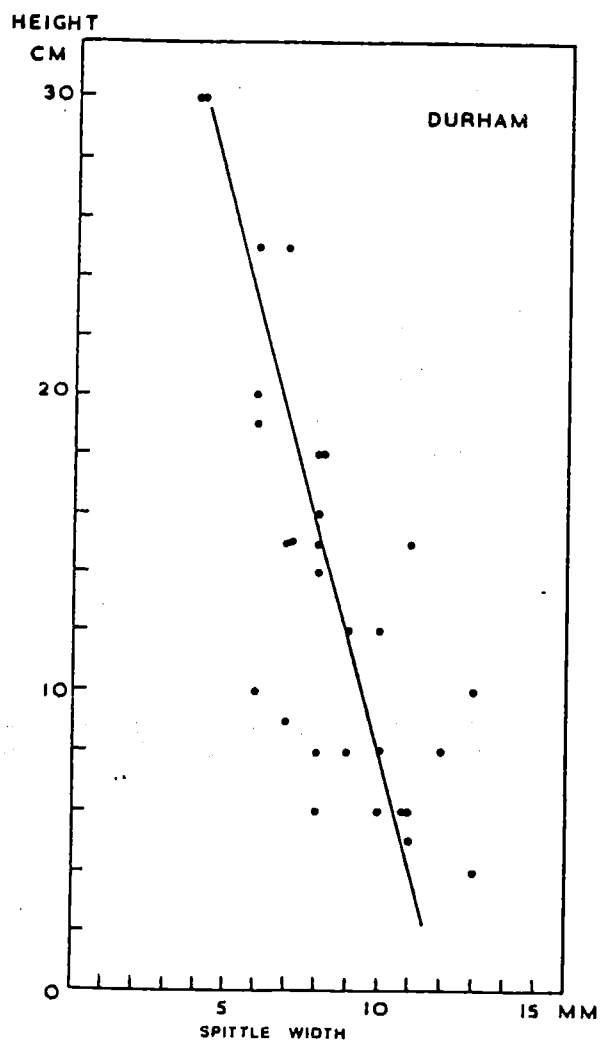


Fig. 2. The relationship between spittle width and its height on the host plant in the laboratory field, University of Durham. ($y = 11.99 - 0.257x$).

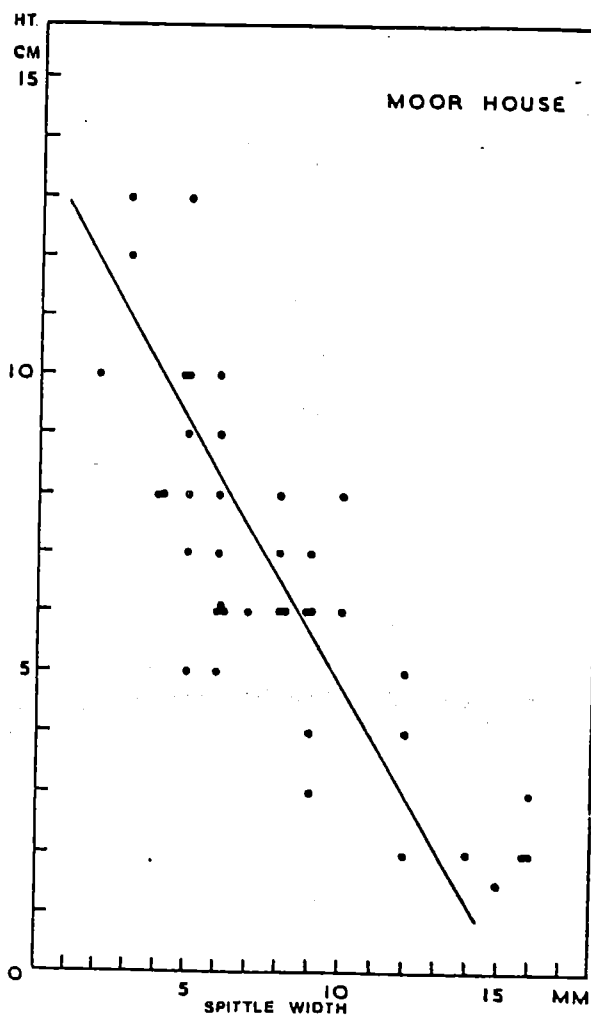


Fig. 3. The relationship between spittle width and its height on the host plant on *Juncus squarrosus* on the Moor House National Nature Reserve. ($y = 15.3 - 1.12x$).

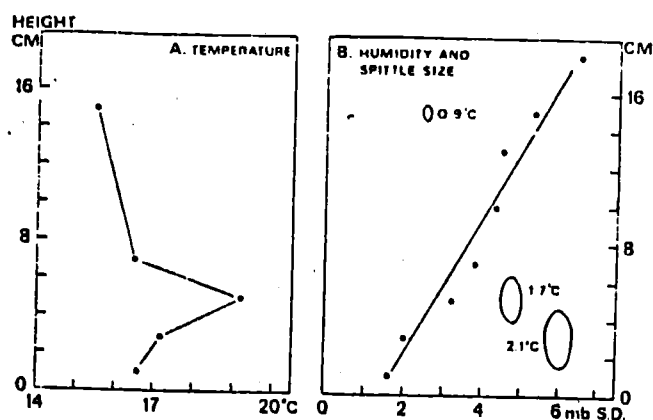


Fig. 4. a) Temperature gradient in *Nardus* on the Moor House National Nature Reserve at 14.00 hrs. on 30 August 1961. b) Humidity gradient in *Nardus* on the Moor House National Nature Reserve at 14.00 hrs. on 30 August 1961. Spittle sizes at different heights are shown diagrammatically and the temperature difference between the centre of the spittle and the surrounding air is given alongside each one.

into instar 5 spittles at three heights in the vegetation. The spittles are shown diagrammatically to scale in Fig. 4B and the temperature difference between the interior of the spittle and the air surrounding it is shown. The spittles closest to the ground surface are the largest and have the greatest insulating effect. Thus although cooling from evaporation will be lower near to the ground surface, this seems to be more than counteracted by the insulating effect of the larger spittles.

5. Acknowledgements

It is a pleasure to thank Professor J. B. Cragg and Dr. J. C. Coulson who supervised the part of this work which was carried out when I was the holder of a Nature Conservancy Research Studentship. Dr. Coulson and Dr. L. Davis also made very useful comments on the manuscript.

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