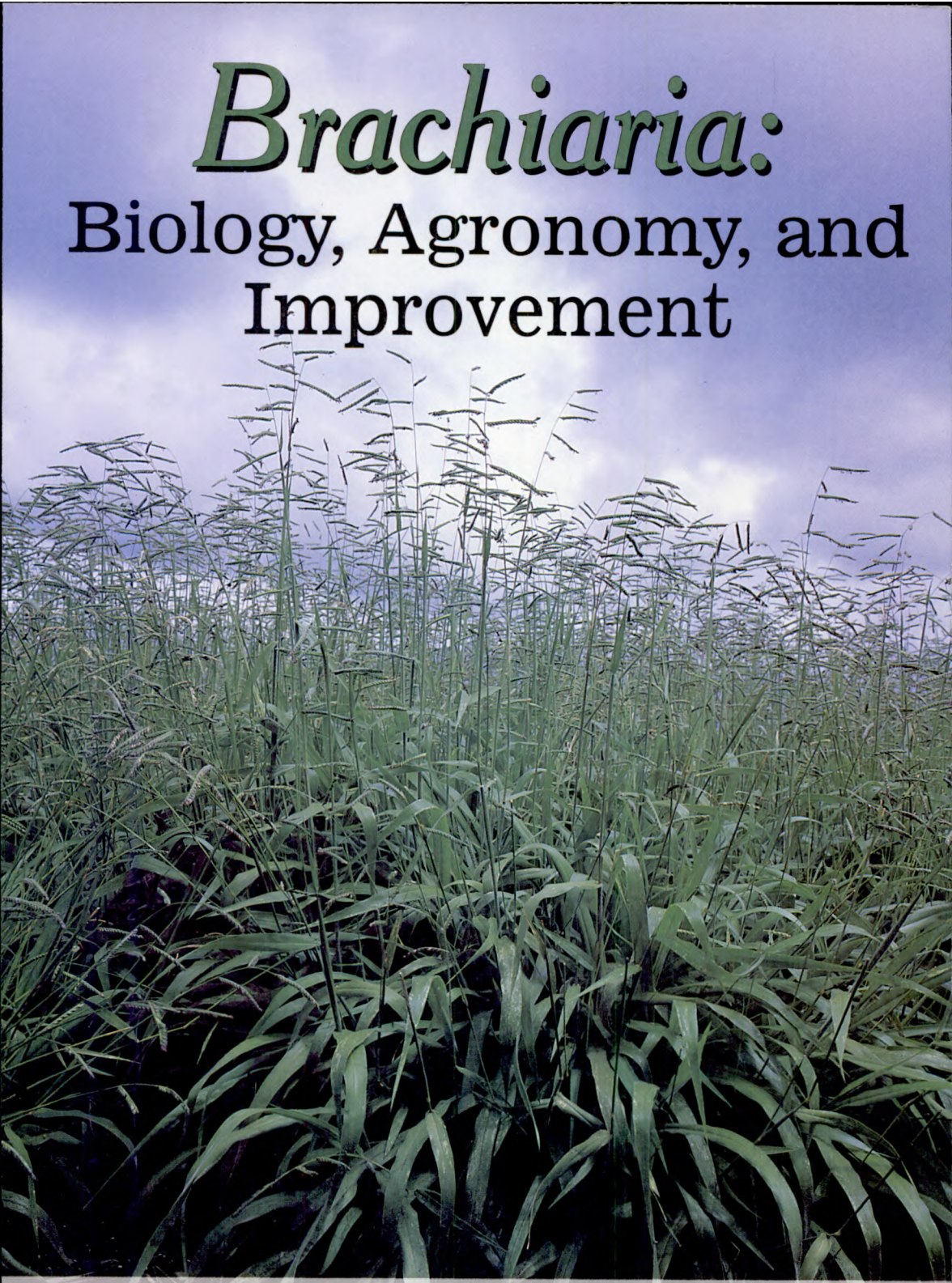
Brachiaria: Biology, Agronomy, and Improvement



Edited by: J. W. Miles, B. L. Maass, and C. B. do Valle,

with the collaboration of
V. Kumble

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Cover photograph:

Brachiaria seed multiplication plot, Popayán, Cauca Department, Colombia.

Photo by Fernando Pino, CIAT.

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Contents

Preface

The economic importance of *Brachiaria* grasses is well established. Estimates of areas currently under *Brachiaria* pastures in Brazil alone range between 30 and 70 million hectares. The forage potential of these grasses was first recognized about 40 years ago, mainly in restricted ecological niches in tropical Australia. The major impact of the genus, however, was realized only in the past 20-25 years, when a handful of *Brachiaria* cultivars, derived directly from naturally occurring germplasm, was widely sown in tropical America. This rapid expansion did not occur without problems, and currently available cultivars are now recognized as having serious defects.

Over the past decade, a greatly enhanced germplasm collection and studies on the cytology and genetics of *Brachiaria* have opened up new opportunities and challenges in the improvement of this important forage.

Accordingly, to clarify current problems and outline a plan for research to enhance the utility of *Brachiaria*, the International Workshop on the Biology, Agronomy, and Improvement of *Brachiaria* was held 3-7 October 1994 at the Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. Workshop participants also reviewed the widely scattered literature and outlined research priorities for this genus—the source of our most important tropical forages.

The Workshop continues a tradition begun in 1982, when an international group of researchers reviewed the biology and agronomy of the genus *Stylosanthes* at a symposium in Townsville, Australia. Since 1982, other important taxa of tropical forage plants have been reviewed in depth: *Centrosema* in 1987 and *Arachis* in 1993. *Andropogon gayanus* was similarly reviewed by researchers in CIAT's (then) Tropical Pastures Program and the results published in 1990.

From the earliest discussions of the idea in 1991, this Workshop was envisioned as a collaborative initiative between EMBRAPA's National Center for Beef Cattle Research (CNPGC, its Portuguese acronym) and CIAT's Tropical Forages Program. Uncertainties of institutional support delayed the workshop for 3 years, until both CIAT and EMBRAPA were able to commit resources to the event. Additional public funding came from the Food and Agriculture Organization of the United Nations (FAO).

The vital economic importance of *Brachiaria* was reflected in a novel development: this was the first workshop in this series to receive generous support from the private sector: commercial seed companies, livestock cooperatives, and commercial beneficiaries of livestock products. This support came, not only as direct monetary contributions, but—perhaps still more significantly—also as active participation in the Workshop's proceedings. This support is gratefully acknowledged.

We were fortunate also to have a wide diversity of participants. The papers presented covered a broad range of topics relating to *Brachiaria*, from the taxonomy of the genus, through genetic manipulation and biotechnology, to the niches being found for *Brachiaria* grasses in different livestock production systems throughout the tropics.

Discussions at the workshop were perhaps more lively than those generated at previous workshops of this kind, which have tended toward agreement among the already converted. This liveliness probably resulted from the participation,

not only of the private sector—which often has a vastly different perception of priorities from that of the public sector researcher—but also of scientists who investigate particular areas, such as biotechnology or nitrogen fixation, in an array of crop species, and who therefore do not have an unquestioning commitment to *Brachiaria*.

The discussions brought to light vital questions that need to be addressed: What is the appropriate role of the private seed companies in *Brachiaria* research and development, and by what institutional and legal mechanisms can this role be made most productive? What are the ecological risks or benefits associated with the planting of many millions of hectares of exotic grasses on the tropical American savannas? These and other questions were addressed in working groups whose reports are compiled in Chapter 18.

We hope that this volume will provide a comprehensive overview of the biology and agronomy of *Brachiaria* and will serve as a guide to researchers whose goal is to realize the fullest potential of these tropical grasses.

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Identifying and Naming Brachiaria *Species*

B. L. Maass*

Knowledge of *Brachiaria*, including that compiled in these proceedings, is based predominantly on one or two genotypes of each species. However, in most of the published literature, particular attributes of these few genotypes are generalized and applied to the whole species. Yet, we are only beginning to appreciate just how diverse this economically important genus is.

Identification

Some genotypes have been widely distributed under an incorrect species name, which continues to cause confusion in the published literature. Thus, detailed morphological, agronomic, and even molecular studies are needed to establish the identity of these materials.

Recent germplasm movements led to some confusion over the identity of accessions that were transferred from the International Livestock Centre for Africa (ILCA) to CIAT by in vitro culture and subsequently distributed to screening sites in tropical America (Keller-Grein et al., Ch. 2, this volume). The correct identification of these materials is being documented and will be published in a germplasm catalog (G. Keller-Grein and B. L. Maass, unpublished data).

The taxonomic position of the various *Brachiaria* species commonly used in pastures is unclear (Boonman, 1993; Loch, 1977). Old names have been perpetuated, causing differences to be regarded as important, whereas similarities are probably more relevant. In addition, some species names that are found in the agronomic literature are now being treated as synonyms (Table 1).

Brachiaria brizantha, *B. decumbens*, *B. eminii*, and *B. ruziziensis*

Brachiaria eminii is closely related to *B. decumbens* and has been confused with it (Renvoize et al., Ch. 1, this volume). In the Congo (now Zaire), *B. decumbens* was cultivated as *B. eminii* (Whyte et al., 1959). According to Boonman (1993), perhaps the names *B. eminii*, *B. decumbens*, and *B. ruziziensis* have all been used for the same material.

Bogdan (1977) stated that *B. ruziziensis* and *B. decumbens* were regarded as closely related. At the Kitale Research Station, Kenya, *B. ruziziensis*

Table 1. Frequently used synonyms of *Brachiaria*.

Correct name	Synonym
B. arrecta (Dur. & Schinz) Stent	*B. radicans* Napp. *B. latifolia* Stapf
B. bovonei (Chiov.) Robyns	*B. viridula* Stapf
B. jubata (Fig. & De Not.) Stapf	*B. soluta* Stapf
B. subquadripara (Trin.) Hitchc.	*B. miliiformis* (J. & C. Presl) Chase
B. subulifolia (Mez) Clayton	*B. falcifera* (Trin.) Stapf

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and *B. brizantha* were not distinguished from each other for a long time.

Brachiaria decumbens was first introduced into Brazil in 1952 under the name *B. brizantha* (Serrão and Simão Neto, 1971). In 1965, material of the same species was acquired from Suriname, this time as *B. decumbens*. These two introductions were both *B. decumbens*, distinct from *B. brizantha*, which was also introduced in 1965.

Similarly, germplasm accessions were selected and propagated for further multilocational testing under incorrect names. For example, accession CIAT 16488 (= BRA-004391), which was initially distributed as *B. decumbens* and frequently cited as such by Pizarro (1992), is now correctly identified as *B. brizantha*.

Renvoize et al. (Ch. 1, this volume) state that the widely used cv. Basilisk, commonly identified as *B. decumbens* (Oram, 1990), is in fact *B. brizantha*. Their statement is supported by C. M. Meghji's finding that the isozyme banding patterns are not typical of *B. decumbens* (1995, personal communication). Because much of the *B. brizantha* germplasm overlaps morphologically with accessions of *B. decumbens*, we will, therefore, tend to continue identifying cv. Basilisk as *B. decumbens*, until the taxonomic status of the whole agamic complex, including *B. brizantha, B. decumbens*, and *B. ruziziensis*, is clarified.

Brachiaria dictyoneura and *B. humidicola*

Skerman and Riveros (1990) consider *B. dictyoneura* a synonym for *B. humidicola*. Bogdan (1977) reported that *B. humidicola* in cultivation is better known as *B. dictyoneura*, and under this name, a productive type was introduced from Rhodesia (now Zimbabwe) into Kenya and other tropical countries. True *B. dictyoneura* is a tufted perennial, whereas *B. humidicola* is strongly stoloniferous.

Several papers in these proceedings refer to *B. dictyoneura*. These references are all to the germplasm that was the origin of cv. Llanero (CPI 59610, CIAT 6133, CPAC 3139, GC 0769, BRA-001449, ILCA 12470, CPI 118939). This accession has been unequivocally identified as *B. humidicola*, based on morphology and on isozyme data (Renvoize et al., Ch. 1, this volume; Keller-Grein et al., Ch. 2, this volume). It is stoloniferous, unlike true *B. dictyoneura*, although less strongly so than *B. humidicola* cv. Tully.

Vernacular Names and Cultivar Names

Spanish and Portuguese abound in vernacular names for *Brachiaria* species, reflecting the agricultural importance of these grasses in tropical America (Table 2). Because Spanish and Portuguese are close to Latin, the scientific name of a species newly introduced into tropical America often became its vernacular name also (e.g., *B. humidicola* as "pasto humidícola") and even its registered cultivar name (e.g., cv. Humidícola) (Pérez B. and Lascano, 1992). However, this conflicts with established rules of nomenclature for cultivated plants (Greuter, 1988) and is confusing as well, since it suggests that this particular material is typical of a species.

Table 2. Vernacular names of *Brachiaria* species.

Brachiaria species	English	Spanish	Portuguese	Other languages[1]
B. arrecta (syn. *B. radicans*)	Tanner grass, tanner-grass	Pasto taner, pasto tanner, taner, tanner	Braquiária do brejo, capim tanner	
B. brizantha	Bread grass, Ceylon sheep grass, palisadegrass, palisade grass, palisade signal grass, signal grass, St. Lucia grass	Brachiaria de Abisinia, estrella de Africa, pasto alambre, pasto señal, señal, zacate señal, zacate signal	Brizantão, brizantha, braquiarão, capim braquiária, capim Marandú, capim ocinde, Marandú	FRA: Signal, signal grass THA: Ya siknaentongtang
B. decumbens	Kenya sheep grass, sheep grass, signalgrass, signal grass, Suriname grass	Braquiaria, decumbens, pasto alambre, pasto braquiaria, pasto chontalpo, pasto de la palizada, pasto de las orillas, pasto peludo, pasto prodigio, zacate prodigio	Australiano, braquiária, braquiária comum, braquiária de alho, capim brachiária, decumbens	MYS: Rumput signal THA: Ya-siknaentonnon, ya-surinam
B. dictyoneura	Coronivia grass			FRA: Koronivia, koronivia grass THA: Ya signal luey
B. distachya	Green summer grass			IDN: Blembem, kadalan, blabakan (Java) MYS: Rumput minyak, rumput melera minyak PHL: Gome-gome, tanageb THA: Yateenka VNM: Co'mât
B. fasciculata	Birdseed grass		Milha dourada	
B. humidicola	Amazonian kikuyu grass, coronivia grass, creeping signal grass, false creeping paspalum, koronivia grass	Braquiaria dulce, humidícola, kikuyu de la Amazonia, pasto dulce, pasto humidícola	Capim agulha, pontudinho, quicuio da Amazônia	THA: Ya humidicola
B. mutica	Angola grass, buffalo grass, Californiagrass, corigrass, cori grass, Dutch grass, giant couch, Mauritius grass, Numidian grass, panicumgrass, Paragrass, Para grass, Penhalonga grass, Scotch grass, watergrass, water grass	Admirable, capin, Egipto, gramalote, grama de Pará, hierba de Pará, hierba del Pará, malohillo, malojillo, Nilo, Pará, Paraná, pasto admirable, pasto de laguna, pasto malojillo, pasto Pará, yerba del parral, zacate Pará	Angola, bengo, capim Angola, capim angolinha, capim Colônia, capim de boi, capim de muda, capim fino, capim de planta, capim de Pará	FRA: Herbe de para, para IDN: Rumput malela, sukut kolonjono, jukut inggris PHL: Babak-nalabaga, mara-kawayan (Ilokano) CMB: Smau kôô THA: Ya khon VNM: Co' lông tây
B. plantaginea	Marmalade grass	Arocillo	Capim marmelada, capim Papua, capim tanner, marmelada, milha branca, milha roxa	

(Continued)

Table 2. (Continued.)

Brachiaria species	English	Spanish	Portuguese	Other languages[1]
B. reptans				FRA: Herbe à bengali
B. ruziziensis	Chinese cabbage, Congo grass, Congo signal, Congo signal grass, Kennedy ruzi, Kennedy ruzigrass, prostrate signal grass, ruzi, ruzigrass, ruzi grass	Congo, Congo señal, gambutera, Kenia, pasto Congo, pasto ruzi, ruzi	Ruziziensis, capim Congo	THA: Ya ruzi
B. subquadripara (syn. *B. miliiformis*)	Cori grass, green summer grass, two-spiked panic, two-finger grass, Thurston grass		Milha preta	

1. CMB = Cambodian; FRA = French; IDN = Indonesian; MYS = Malay; PHL = Filipino; THA = Thai; VNM = Vietnamese.

SOURCES: Mejía M., 1984; Toutain, 1989; Skerman and Riveros, 1990; 't Mannetje and Jones, 1992.

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Chapter 1

Morphology, Taxonomy, and Natural Distribution of *Brachiaria* (Trin.) Griseb.

S. A. Renvoize,* W. D. Clayton,* and C. H. S. Kabuye**

Abstract

We reviewed 97 species of the genus *Brachiaria*, spanning the whole taxon. The species were arranged in groups according to perceived natural affinities. The morphology of the inflorescence, especially the spikelet, was examined in detail and found to be highly variable; accordingly, the number of options for possible alliances among the species is particularly large. Although we eventually established a framework based on nine groups, their boundaries are as yet tentative, with 14 species still to be adequately grouped. The relationship of *Brachiaria* with other close genera is also discussed.

Introduction

Trinius (1834) described *Brachiaria* as a subdivision of *Panicum*; Grisebach (1853) elevated Trinius' subdivision to the category of genus. *Brachiaria* is now a large genus that contains about 100 species distributed throughout the tropics, especially in Africa. They grow in a wide range of habitats—from swamps to light forest shade to semidesert—but most species are typically found in savannas. Many species also occur as weeds in crops, along roadsides, and in other disturbed places. Agronomic interest in this genus has centered on the use of several species for tropical pasture development, particularly *B. decumbens*, which has proved outstanding in its performance compared with other tropical pasture grasses.

This study demonstrated the highly diverse nature of the constituent species and highlights the enigmatic status of the genus *Brachiaria* in terms of both its component species and its relationships with other genera. The taxonomy is far from satisfactory, and although recently various workers have sought to clarify the situation in specific regions—notably Morrone and Zuloaga (1992), Thompson and Estes (1986), and Webster (1987)—none has provided satisfactory solutions to the problems of generic identity and species composition across the entire taxon.

This survey was based on the resources of the World Grasses Database and the Herbarium and Library of the Royal Botanic Gardens (RBG), Kew, UK. The objectives were twofold:

1. Investigate the boundaries of *Brachiaria* with other related genera in the tribe Paniceae.

2. Review the genus on a global scale to understand the morphological variation within it.

The Genus

Within the tribe Paniceae, the principal characters that identify the genus *Brachiaria* are ovate or oblong spikelets, arranged in one-sided racemes, with the lower glume adjacent to the rachis (RBG, unpublished data). These characters, however, are by no means consistent throughout the genus, and in those species in which the spikelets are paired and borne on a triquetrous rachis, the orientation of the spikelets is often difficult to determine.

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Brachiaria belongs to a small group of genera that includes *Urochloa*, *Eriochloa*, and *Panicum* (Figure 1). All have the PEP-CK (phosphoenolpyruvate carboxykinase) type of C_4 photosynthetic pathway (Clayton and Renvoize, 1986) and, although they have been recognized for over 100 years, the precise boundaries of these genera are still in doubt. *Urochloa* is scarcely separable from *Brachiaria*, differing in little but the orientation of the spikelets (Figure 1A). The recent argument for combining these two genera is discussed later. *Eriochloa* is a homogeneous genus distinguished by its bead-like callus (Figure 1E); it is clearly a derivative of *Brachiaria*, some of whose species have a stipitiform callus that foreshadows this transformation. The discoid pedicel tip, which frequently occurs in *Brachiaria*, is also typical of *Eriochloa*. A few species of *Brachiaria* have a nipped tip to the upper lemma and may be difficult to separate from *Acroceras*, but this is a matter of mimicry easily resolved by studying the leaf-blade anatomy, which in *Acroceras* is C_3. The real problem arises in separating *Brachiaria* from *Panicum*, as discussed later.

Figure 1. *Urochloa trichopus*: (A) Racemes x 2; (B) Spikelet, viewed from the lower glume x 10; (C) Upper floret x 10.
Eriochloa fatmensis: (D) Racemes x 2; (E) Spikelet x 10; (F) Upper floret x 10.
Panicum repens: (G) Inflorescence x 2; (H) Spikelet, viewed from the lower glume x 10; (J) Upper floret x 10.
P. stoloniferum: (K) Part of inflorescence x 2. *Brachiaria decumbens*: (L) Part of raceme x 2.
B. deflexa: (M) Part of raceme x 2; (N) Spikelet, viewed from the lower glume x 10; (P) Upper floret x 10.

The Species

No adequate revision of *Brachiaria* is available, although a sectorial classification was proposed by Stapf (1919) for 56 African species and for the world by Pilger (1940) for 50 species.

For a genus of this size, which has been recognized for over 100 years, it is surprising that no natural subdivisions, based on an overall review of the taxon, have been recognized. This may be because of the confusion over the boundary with *Panicum*, leading different authors to exchange species between these two genera. The equivocal position of many species only highlights the growing theory that *Brachiaria* possibly evolved from several different groups of *Panicum* (RBG, unpublished data). The genus seems to comprise an amalgamation of disparate groups whose circumscription until now has been largely the result of conjecture.

The traditional image of *Brachiaria* is based on common species, such as *B. brizantha* and *B. arrecta*, which have relatively large and oblong or elliptic spikelets 3-6 mm long, arranged in a regular row along one side of a flattened, ribbon-like rachis. However, many species do not conform to this pattern. This survey, which uses morphological characters, has revealed a remarkable diversity that results in many permutations of seemingly significant features. Such diversity makes correlations difficult, and, to a certain extent, explains why previous workers were unable or reluctant to establish credible infrageneric divisions. Groups can be identified, but they often intergrade.

In our study, we sorted the species into nine groups according to character associations. This left only a few species ungrouped. Deciding which characters are of the greatest significance as indicators of natural affinity proved difficult, and the choice was, to a large extent, arbitrary and based on our experience. Table 1 shows the characters

Table 1. Most significant characters chosen for assessing relationships among *Brachiaria* species.

Character	Expression
Spikelet outline shape (Figures 2E-2L)	a. Ovate, obovate, acute, or acuminate b. Oblong and blunt c. Orbicular and blunt
Spikelet three-dimensional shape	a. Turgid, usually associated with a triquetrous rachis b. Flattened, usually associated with a flat rachis
Lower glume relative length (Figures 2E, 2F, 2G, and 2L)	a. Up to half the length of the spikelet b. Two-thirds to three-fourths the length of the spikelet
Lower glume shape	a. Cuff-like (short and clasping, Figure 2K) b. Ovate and flattened (not clasping, Figure 2L)
Internode	a. Present between lower glume and upper glume (Figure 2H) b. Absent
Stipe	a. Present, usually associated with a cuff-like lower glume b. Absent
Upper glume and lower lemma	a. With linear veins only b. With reticulate veins throughout their length (Figure 2K)
Rachis in cross section (Figures 2M, 2N, and 2P)	a. Triquetrous b. Ribbon-like and either narrow or winged c. Crescentic
Upper lemma (Figures 2A, 2B, 2C, and 2D)	a. Smooth and shining b. Striate, rugulose, or rugose

Table 2. Secondary characters for assessing relationships among *Brachiaria* species.

Character	Expression
Racemes	Few to many Spread out on a long axis or congested on a short axis
Pedicels	Long or short Appressed or spreading
Spikelets	Solitary, paired, or clustered Dense or lax on the rachis Size Hairy or not hairy

chosen as the most significant in assessing relationships among species. Table 2 shows those characters which, although they impart a distinctive appearance to a species, are considered to be of secondary importance as indicators of natural affinity. The groups are described below; in their species lists, anomalous or noteworthy characters are placed in parentheses.

A full list of the species examined is given in the Appendix. Descriptions and distribution information for all the species are available on request to the first author.

Group 1

Group 1 (38 species) is characterized by the triquetrous rachis and irregular arrangement of the spikelets. The adaxial position of the lower glume, which characterizes the genus, is not clear in those species that bear paired spikelets on long pedicels. The group intergrades with Groups 3 and 4 through *B. leersioides*.

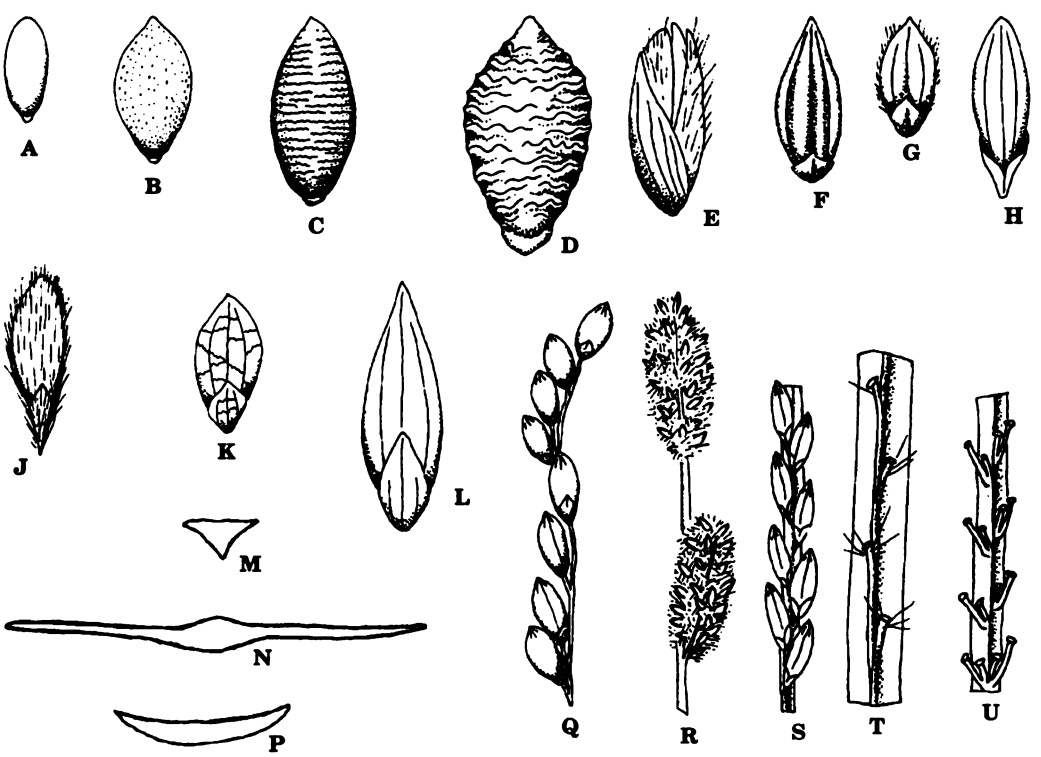

Figure 2. Upper florets x 20: (A) *Brachiaria eruciformis*; (B) *B. glomerata*; (C) *B. arrecta*; (D) *B. grossa*. Spikelets x 15: (E) *B. jubata*; (F) *B. reptans*; (G) *B. semiundulata*; (H) *B. humbertiana*; (J) *B. pungipes*; (K) *B. fasciculata*; (L) *B. arrecta*. Transverse section of rachis x 20: (M) *B. grossa*; (N) *B. ruziziensis*; (P) *B. brizantha*. Inflorescence: (Q) *B. grossa*, x 4; (R) *B. glomerata*, x 2; (S) *B. subquadripara*, x 4. Part of rachis with spikelets removed: (T) *B. arrecta*, x 10; (U) *B. marlothii*, x 10.

Racemes: few to many along a central axis, branchlets sometimes present in the lower part of the raceme. *Rachis:* triquetrous (Figure 2M); spikelets dense or lax and appressed to the rachis, progressing to spikelets lax, with pedicels long, spreading, solitary, paired, or in clusters. *Spikelets:* ovate, obovate/oblong, acute, or obtuse, 1.5-4.0 mm long. *Lower glume:* ovate, up to half the length of the spikelet, cuff-like, sometimes weakly so (Figure 2F). *Upper lemma:* rugose, rugulose, or papillose/granulose.

This group is divided into two subgroups, based on the facies of the racemes.

Subgroup 1A. *Pedicels:* short (Figure 2Q). *Spikelets:* dense, often appressed.

African species:

B. bemarivensis (upper lemma smooth).
B. breviglumis (spikelets elliptic).
B. comata (spikelets 1.5 mm long; upper lemma papillose).
B. coronifera (spikelets elliptic).
B. grossa.
B. lata.
B. leersioides.
B. nana (racemes short, comprising a few spikelets enclosed in the uppermost sheath).
B. orthostachys (spikelets paired, in two dense rows).
B. ovalis (spikelets stipitate).
B. reptans (spikelets paired, not appressed; lower glume very short).
B. scalaris (spikelets elliptic).
B. serpens (spikelets 2 mm long; inflorescence reduced to a cluster of four to eight paired spikelets).
B. serrifolia.
B. umbratilis (spikelets clustered).
B. villosa (spikelets solitary, in two rows, not appressed; upper lemma papillose/rugulose).

American species:

B. adspersa (pedicels discoid tipped; spikelets not stipitate).
B. arizonica.
B. echinulata (spikelets not stipitate).
B. fasciculata (upper glume and lower lemma with conspicuous cross veins, mostly toward the apex; Figure 2K).
B. lorentziana (pedicels discoid tipped).
B. mollis (spikelets solitary or paired, in two rows).
B. texana (spikelets solitary or paired; pedicels discoid tipped).

Australian and Asian species:

B. foliosa (spikelets 5 mm long, stipitate; upper lemma weakly rugulose, apiculate).
B. nilagirica (lower glume two-thirds to three-fourths the length of spikelet; spikelets obovate, paired or in clusters, dense; racemes irregular; upper lemma papillose).
B. polyphylla.
B. praetervisa.
B. pubigera (lower lemma coriaceous).

Subgroup 1B. *Pedicels:* unequal, at least one pedicel in a pair long and spreading (Figure 1M). *Spikelets:* lax, not appressed to the axis.

African species:

B. chusqueoides.
B. deflexa.
B. humbertiana (spikelets oblong, stipitate, internode present; Figure 2H).
B. lindiensis (spikelets stipitate).
B. longiflora (spikelets stipitate, 7 mm long; upper lemma smooth, blunt).
B. ramosa (intergrades on pedicel length with Group 1A).

American species:

B. megastachya (spikelets oblong, solitary, paired or in threes on long and short pedicels; lower glume cuff-like, stipitate, internode present; inflorescence very lax).

Asian species:

B. kurzii.
B. remota (spikelets stipitate).
B. semiverticillata.

Group 2

Group 2 (eight species, from Africa only) is similar in many ways to Group 1, but is separated primarily by its pilose spikelets, although this is probably an artificial distinction.

Racemes: few to many, long or short, generally appressed or ascending, scattered along the central axis, rarely congested. *Rachis:* triquetrous. *Spikelets:* solitary or paired, on short pedicels, in two dense regular rows, not appressed, villous or pilose. *Lower glume:* not cuff-like. *Upper lemma:* smooth, papillose/granular, or finely rugose.

African species:

B. ambigens (pedicels discoid tipped).
B. glomerata (racemes short; spikelets irregularly arranged, congested, Figure 2R; pedicels paired discoid tipped; upper lemma shiny, striate, smooth, Figure 2B; rachilla extension present).
B. lachnantha.
B. mesocoma (sometimes assigned to the genus *Leucophrys*; lower glume as long as spikelet; upper glume and lower lemma acuminate, with a band of hairs half-way up; pedicels discoid tipped).
B. nigropedata.
B. psammophila (pedicels discoid tipped; racemes irregular; spikelets congested; lower glume one-half to two-thirds the length of spikelet).
B. serrata (spikelets suborbicular, elliptic but not stipitate; pedicels discoid tipped).
B. xantholeuca (lower glume cuff-like; racemes rather lax).

Groups 3 and 4

Group 3 (five species) and Group 4 (eight species) have a distinctive appearance, largely because of the flat, ribbon-like rachis, which imposes more order on the arrangement of the spikelets in the raceme than in Group 1. The spikelets are on short pedicels in neat rows, and are either dense and at an angle or spread out and appressed. The resulting orderly appearance contrasts with the often rather irregular appearance of racemes in Group 1. The decision to recognize two groups here, despite the many similarities, is based on differences in the shape of the lower glume.

Group 3. *Racemes:* two to many, scattered along a central axis, spreading. *Rachis:* flat, narrow. *Spikelets:* solitary, narrowly ovate, not turgid; pedicels short (Figures 2L and 2T). *Lower glume:* ovate, flat, not stipitate at the base. *Upper lemma:* rugulose, no mucro.

African species:

B. arrecta.
B. distachyoides.
B. mutica (spikelets paired or clustered on the rachis, otherwise similar to *B. arrecta*).
B. rugulosa (spikelets dense).

American species:

B. platyphylla.

Group 4. *Racemes:* two to several, usually scattered along a central axis, ascending or spreading. *Rachis:* narrow, bearing solitary spikelets on short pedicels; spikelets appressed and lax (Figure 2S) or spreading and dense. *Spikelets:* ovate or narrowly ovate, turgid or compressed. *Lower glume:* cuff-like, stipitate. *Upper lemma:* rugulose.

African species:

B. distachya.
B. plantaginea.
B. pseudodichotoma (racemes solitary or paired; subconjugate).
B. subquadripara.

American species:

B. meziana (racemes congested; lower glume weakly cuff-like, not stipitate; rachis very narrow; upper lemma mucronate).

Asian species:

B. burmanica.

Australian species:

B. piligera.
B. whiteana.

Groups 5 and 6

Group 5 (six species) and Group 6 (nine species) are both African, and are allied through their elliptic oblong spikelet shape but maintained as two separate groups on the basis of (1) the length of the lower glume, which may be very short and cuff-like as opposed to almost as long as the spikelet, and (2) the presence or absence of reticulate venation in the upper glume and lower lemma. Rachis shape ranges from triquetrous to winged.

Group 5. *Racemes:* few to several, scattered along a central axis, ascending or spreading (Figure 1L). *Rachis:* broad or narrow, ribbon-like (Figure 2N) or crescentic (Figure 2P), one-sided; spikelets solitary, on short pedicels, forming one or two distinct rows, dense, spreading (Figure 1L). *Spikelets:* large, 3.5-6.0 mm long, ovate or oblong, turgid. *Lower glume:* cuff-like. *Upper lemma:* granulose.

African species:

B. brizantha (rachis narrow, crescentic; Figure 2P)
B. decumbens (rachis ribbon-like; upper lemma nipped at the tip).
B. dura (racemes one to two; rachis narrow, crescentic; lower glume not cuff-like; pedicels discoid tipped; included in Group 5 on the basis of spikelet shape).
B. eminii (rachis ribbon-like; internode present; upper lemma papillose or rugulose, apiculate).
B. oligobrachiata (rachis ribbon-like; spikelets lanceolate; upper lemma nipped at the tip).
B. ruziziensis (rachis broadly winged, Figure 2N; upper lemma striate).

This group includes the three most important species currently used for pasture development: *B. brizantha*, *B. decumbens*, and *B. ruziziensis*. The first two species are closely related and at times difficult to distinguish. *Brachiaria ruziziensis* may be identified by its exceptionally broad, winged rachis, 2.0-3.5 mm wide; *B. decumbens* likewise has a winged rachis, 1.0-1.7 mm wide. In both these species, the spikelets are borne in two rows, and the glumes and lower lemma are membranous in texture. *Brachiaria brizantha* has a crescentic rachis that is seldom more than 1 mm wide; the spikelets are borne in a single row; and the glumes and lower lemma are cartilaginous in texture. Furthermore, it is distinguished from the other two species by its erect, tufted habit and often much longer leaf blades. *Brachiaria decumbens* and *B. ruziziensis* are both decumbent in habit and have lanceolate leaf blades.

Brachiaria brizantha and *B. decumbens* are inclined to intergrade in their vegetative features, and ambiguous specimens may be distinguished only by the rachis shape and spikelet arrangement and texture. The most widely grown genotype, cv. Basilisk (CIAT 606), which is currently being used in hybridization programs at CIAT and EMBRAPA, was originally identified as *B. decumbens*, but after reassessment was reidentified as *B. brizantha*.

Brachiaria eminii is also closely related and has been confused with *B. decumbens*; it is most readily distinguished by its annual habit. Other differences are the 3-10 racemes in the inflorescence; a slightly longer lower glume, one-half to two-thirds the length of the spikelet; and a mucronate upper lemma.

Group 6. *Racemes:* one to four scattered on the central axis, ascending or spreading. *Rachis:* flat, broad, narrow, or almost triquetrous. *Spikelets:* elliptic or oblong. *Lower glume:* over two-thirds the length of the spikelet, many nerves (Figure 2E). *Upper glume and lower lemma:* nerves reticulate. *Upper lemma:* granulose, papillose, striate, or smooth.

African species:

B. bovonei (rachis almost triquetrous).
B. brevispicata (lower glume with few nerves; upper lemma rugulose).
B. dictyoneura (racemes 3-15; rachis very narrow, almost triquetrous).
B. humidicola (upper lemma nipped at the tip, rachis very narrow, almost triquetrous).
B. jubata.
B. platynota.
B. reticulata (spikelets obovate; lower glume half the length of the spikelet; inclusion in Group 6 on the basis of the reticulately nerved upper glume and lower lemma).
B. stigmatisata.
B. subulifolia (syn. *B. falcifera*) (upper lemma nipped at the tip).

Two species of this group have been used for sown pastures: *B. dictyoneura* and *B. humidicola*. They are closely related and, at times, have been confused by agronomists. The name *B. humidicola* is correctly applied to plants that are stoloniferous; *B. dictyoneura*, to those tufted in habit. Some confusion arose when a stoloniferous plant, that is, *B. humidicola*, was distributed from Rhodesia (now Zimbabwe) for pasture development under the name *B. dictyoneura* (Bogdan, 1977). Accession CIAT 6133 is correctly identified as *B. humidicola*: it has stolons, wiry culms, and three racemes in the inflorescence. In the past, this accession was wrongly identified as *B. dictyoneura* and has been widely distributed under that name. Accession CIAT 16508, which is identified as *B. dictyoneura*, appears to be intermediate between the two species. CIAT 16508 has the slender base, narrow leaf blades, and three racemes typical of *B. humidicola*, but, as this species intergrades on these characters with *B. dictyoneura*, the deciding factors are the lack of stolons and the apparently tufted habit, which place it in *B. dictyoneura*.

Group 7

Group 7 (three species) is also African. All three species are characterized by an obtuse, smooth upper lemma, which is considered by Webster (1987) to be sufficiently distinct to merit generic status.

Racemes: 3-15, scattered on a central axis. *Rachis:* very narrow, wingless. *Spikelets:* elliptic-oblong. *Lower glume:* very small. *Upper lemma:* smooth, blunt, no mucro (Figure 2A); easily disarticulates.

African species:

B. eruciformis.
B. malacodes (inflorescence a panicle, the delicate branches tipped with short racemes).
B. schoenfelderi.

Group 8

Group 8 (three species) has spikelets with a pungent callus, in all the other species the callus is blunt or square. It is curious that in this group the species are so widely dispersed; two are African (Zambia and Zaire) and one is from northern Australia. This suggests that the choice of the callus as the prime means of identification may be ill judged; however, it is an outstanding feature throughout the grass family and can hardly be ignored here.

Racemes: 3-10, scattered on a central axis, appressed. *Rachis:* triquetrous. *Spikelets:* obovate. *Lower glume:* ovate, flat. *Upper lemma:* smooth or papillose/striate, with broad overlap around the upper palea, apiculate. *Callus:* oblique, pungent (Figure 2J).

African species:

B. pungipes (spikelets paired, dense; internode between lower glume and upper glume).

B. turbinata (spikelets paired, dense; no internode).

Australian species:

B. argentea (spikelets solitary, lax; no internode).

Group 9

Group 9 (three species) has characteristic villous margins to the upper glume and lower lemma, which give these species a highly distinctive appearance. Two species are American, one is Australian—a strange alliance, as was noted by Chase (1920).

Racemes: two to five, scattered on a central axis, appressed or spreading. *Rachis:* very narrow, wingless; pedicels short, solitary or paired, bearing spikelets in two rows. *Spikelets:* ovate. *Upper glume and lower lemma:* with densely villous margins. *Upper lemma:* rugose or rugulose.

American species:

B. ciliatissima (lower glume weakly cuff-like at the base, two-thirds the length of the spikelet; upper glume villous on the back).

B. ophryodes (lower glume half the length of the spikelet, weakly cuff-like; upper glume pubescent on the back; lower lemma glabrous in the center; upper lemma mucronate).

Australian species:

B. gilesii (racemes congested; spikelets dense, on a ribbon-like rachis, solitary; lower glume a very short scale, not cuff-like; upper glume pilose; lower lemma villous on the margins; upper lemma mucronate).

Ungrouped species

Fourteen species have been left ungrouped. These are listed below, with descriptions of the distinctive characters of each.

African species:

B. antsirabensis (spikelets suborbicular; upper lemma smooth; lower glume short, not cuff-like; granular or spiculate surface to the glumes and lower lemma; upper glume sparsely pilose, nerves obscure; racemes short; spikelets 3 mm).

B. clavipila (upper lemma smooth, pubescent at the tip; glumes and lower lemma with seven to nine nerves).

B. epacridifolia (leaves short; racemes reduced to two paired, solitary spikelets; lower glume cuff-like).

B. leucacrantha (spikelet acuminate, solitary; lower glume cuff-like, stipitate).

B. marlothii (rachis flat; spikelets paired, Figure 2U).

B. perrieri (rachis triquetrous; spikelets solitary, irregular, villous; upper glume and lower lemma with a transverse fringe of hairs; lower lemma shortly awned).

B. semiundulata (spikelets solitary, in two rows, not appressed, obovate, Figure 2G; lower glume very short, not cuff-like; upper lemma papillose striate).

B. subrostrata (spikelets solitary; lower glume a short scale; a band of hairs in the top half of upper glume and lower lemma).

B. umbellata (spikelets oblong, solitary; lower glume very small; upper lemma smooth, acute).

American species:

B. paucispicata (lower glume one-half to two-thirds the length of the spikelet, not cuff-like, internode present, stipitate).

B. tatianae (rachilla extension present).

Asian species:

B. tanimbarensis (spikelets in two neat rows on a ribbon-like rachis, solitary, dense, not appressed).

Australian species:

B. advena (rachis triquetrous; racemes short, appressed; spikelets oblong, dense on the rachis in two neat rows, lower glume very short, cuff-like).

B. holosericea (lower glume short, scale-like, nerveless, not cuff-like; upper lemma papillose/striate, apiculate; upper glume and lower lemma with a line of long hairs across the middle; spikelets obovate, solitary; rachis triquetrous; pedicels discoid tipped, in one or two rows).

Discussion

Brachiaria and *Urochloa*

Webster (1987), in an account on Australian grasses, transferred many species from *Brachiaria* to *Urochloa*. His argument was that those species in which the upper floret disarticulates from the rest of the spikelet deserved recognition as a distinct genus, separate from those species which disarticulates below the lower glume. The species that he identified as having the former characteristic was *B. eruciformis*, and, because this is the type species for the genus *Brachiaria*, then this name remains with the redefined group of species. Thus, all those species formerly in *Brachiaria* but separated by Webster (1987) on the basis of disarticulation below the lower glume are left requiring a new generic location. Webster placed them in *Urochloa*, arguing that the rejected species were identified not only by their disarticulation below the lower glume, but also by their mucronate upper floret, and therefore had a close similarity to *Urochloa*. Morrone and Zuloaga (1992) followed Webster and transferred all the indigenous South American species of *Brachiaria* to *Urochloa*.

Therefore, according to Webster (1987) and Morrone and Zuloaga (1992), the discriminatory characters for the two genera are as follows:

Brachiaria. *Upper floret:* smooth, shiny, not constricted at the base, blunt and without a mucro, disarticulating at the base; upper palea free at the tip. *Lower glume:* very small, one-sixth to one-fifth the length of the spikelet.

Urochloa. *Upper floret:* finely to coarsely transverse rugose, apiculate to mucronate; upper palea enclosed at the tip by the lemma. *Lower glume:* small to large, one-fourth as long as the spikelet, often cuff-like and clasping. *Spikelet:* disarticulating at the base of the lower glume.

Traditionally, *Urochloa* was distinguished from *Brachiaria* by the orientation of its spikelets, with the upper glume adjacent to the axis. But spikelet orientation becomes indeterminate when spikelets are paired, as in some *Urochloa* species, or are on long pedicels, as in some *Brachiaria* species. This means differentiating *Urochloa* on the basis of its planoconvex, cuspidate spikelets (which may also occur in *Brachiaria*) and mucronate upper lemma (Figures 1B and 1C). But numerous species of *Brachiaria* have an apiculate upper lemma, and several species, such as *B. gilesii* and *B. ophryodes* have a mucro up to 1 mm long.

While, on the one hand, these characters certainly circumscribe a group of allied species and the two genera could well be united under the older name *Urochloa*, on the other hand, the placing of marginal species is open to subjective interpretation. In addition, the deciduous upper lemma does deserve recognition and the name *Brachiaria* could therefore be retained for those three species that have the deciduous upper lemma; but this is not a satisfactory solution.

Brachiaria and *Panicum*

The distinction of *Brachiaria* with racemes from *Panicum* with panicles is simply resolved in the African species (Figure 1G). In the Americas, however, it breaks down, as some species, such as *P. pilosum* and *P. stoloniferum* (Figure 1K), have condensed panicles and are raceme-like. Conversely, some American *Brachiaria* species, such as *B. deflexa* (Figure 1M) and *B. ramosa*, have loose racemes that are panicle-like. In most cases, where the inflorescence facies appears to transgress traditional generic boundaries, some additional characters peculiar to *Brachiaria*—such as shape of the spikelets, a stipitate base, or a cuff-like lower glume—aid identification. The matter, however, will not be completely resolved until the American *Panicum* species are adequately revised.

The photosynthetic biochemical characterization of *Brachiaria* is PEP-CK, and any links with *Panicum* should be sought in that sector of the genus with similar anatomy for the PEP-CK photosynthetic pathway. Recent investigations into the photosynthetic diversity of the Paniceae, however, suggest that the C_4 pathway has probably evolved independently on several occasions (Hattersley and Watson, 1992; Renvoize, 1987).

In several recent works, opinions differ as far as generic circumscription is concerned; Simon (1993), for instance, favors the original concept of *Brachiaria*, whereas Davidse and Pohl (1994) have taken up Webster's proposals (1987). For practical purposes, retaining, for now, the traditional concept of *Brachiaria* would be preferable, despite the arguments of Webster (1987) and Morrone and Zuloaga (1992). But the genera under discussion are certainly very closely related, and lines between them can be drawn only with difficulty.

The problems of differentiation, caused by substantial variations in seemingly significant generic characters, are also found in other genera. For example, in *Pennisetum*, the section *Brevivalvula* has a readily deciduous, shining, obtuse upper floret, in contrast to other sections of the genus. Other species within larger genera with this feature are *Melinis repens*; *Panicum*, sect. Veruculosae; and *P. cervicatum*.

Conclusion

Although this review has thrown little light on the interrelationships of species in *Brachiaria*, it has indicated where the problems lie—the first step toward resolving them. A detailed statistical analysis of morphology may provide a sound system of classification for the genus, but other sources of data will have to be sought. Further investigations of leaf-blade anatomy and chemical and molecular analyses may help resolve some of the enigmas and reveal natural patterns or species alliances within the genus.

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Appendix. *Brachiaria* Species by Continent of Origin.

Brachiaria species are arranged in alphabetical order by continent of origin. They are tentatively clustered into nine groups, with 14 species still outstanding.

African species	Group no.
B. ambigens Chiov.	2
B. antsirabensis A. Camus	Ungrouped
B. arrecta (Dur. & Schinz) Stent	3
B. bemarivensis A. Camus	1
B. bovonei (Chiov.) Robyns	6
B. breviglumis Clayton	1
B. brevispicata (Rendle) Stapf	6
B. brizantha (A. Rich.) Stapf	5
B. chusqueoides (Hack.) Clayton	1
B. clavipila (Chiov.) Robyns	Ungrouped
B. comata (A. Rich.) Stapf	1
B. coronifera Pilg.	1
B. decumbens Stapf	5
B. deflexa (Schumach.) Hubbard	1
B. dictyoneura (Fig. & De Not.) Stapf	6
B. distachya (L.) Stapf	4
B. distachyoides Stapf	3
B. dura Stapf	5
B. eminii (Mez) Robyns	5
B. epacridifolia (Stapf) A. Camus	Ungrouped
B. eruciformis (J. E. Smith) Griseb.	7
B. glomerata (Stapf) A. Camus	2
B. grossa Stapf	1
B. humbertiana A. Camus	1
B. humidicola (Rendle) Schweick.	6
B. jubata (Fig. & De Not.) Stapf	6
B. lachnantha (Hochst.) Stapf	2
B. lata (Schumach.) Hubbard	1
B. leersioides (Hochst) Stapf	1
B. leucacrantha (K. Schum.) Stapf	Ungrouped
B. lindiensis (Pilg.) Clayton	1
B. longiflora Clayton	1
B. malacodes (Mez & K. Schum.) Scholz	7
B. marlothii (Hack.) Stent	Ungrouped
B. mesocoma (Nees) A. Camus	2
B. mutica (Forssk.) Stapf	3
B. nana Stapf	1
B. nigropedata (Ficalho & Hiern) Stapf	2
B. oligobrachiata (Pilg.) Henr. (syn. *B. platytaenia* Stapf)	5
B. orthostachys (Mez) W. D. Clayton	1
B. ovalis Stapf	1

(Continued)

Appendix. (Continued.)

	Group no.
B. perrieri A. Camus	Ungrouped
B. plantaginea (Link) Hitchc.	4
B. platynota (K. Schum.) Robyns	6
B. psammophila (Welw. ex Rendle) Launert	2
B. pseudodichotoma Bosser	4
B. pungipes Clayton	8
B. ramosa (L.) Stapf	1
B. reptans (L.) Gardner & Hubbard	1
B. reticulata Stapf	6
B. rugulosa Stapf	3
B. ruziziensis Germain & Evrard	5
B. scalaris Pilg.	1
B. schoenfelderi Hubbard & Schweick.	7
B. semiundulata (A. Rich.) Stapf	Ungrouped
B. serpens (Kunth) Hubbard	1
B. serrata (Thunb.) Stapf	2
B. serrifolia (Hochst.) Stapf	1
B. stigmatisata (Mez) Stapf	6
B. subquadripara (Trin.) Hitchc.	4
B. subrostrata A. Camus	Ungrouped
B. subulifolia (Mez) Clayton	6
B. turbinata Van der Veken	8
B. umbellata (Trin.) Clayton	Ungrouped
B. umbratilis Napper	1
B. villosa (Lam.) A. Camus	1
B. xantholeuca (Schinz) Stapf	2
American species	
B. adspersa (Trin.) Parodi	1
B. arizonica (Scribn. & Merr.) S. T. Blake	1
B. ciliatissima (Buckl.) Chase	9
B. echinulata (Mez) Parodi	1
B. fasciculata (Swartz) Parodi	1
B. lorentziana (Mez) Parodi	1
B. megastachya (Nees ex Trin.) Zuloaga & Soderstrom	1
B. meziana Hitchc.	4
B. mollis (Swartz) Parodi	1
B. ophryodes Chase	9
B. paucispicata (Morong) Clayton	Ungrouped
B. platyphylla Nash	3
B. tatianae Zuloaga & Soderstrom	Ungrouped
B. texana (Buckl.) S. T. Blake	1

(Continued)

Appendix. (Continued.)

	Group no.
Australian species	
B. advena Vickery	Ungrouped
B. argentea (R. Br.) Hughes	8
B. foliosa (R. Br.) Hughes	1
B. gilesii (Benth.) Chase	9
B. holosericea (R. Br.) Hughes	Ungrouped
B. piligera (F. Muell.) Hughes	4
B. polyphylla (R. Br.) Hughes	1
B. praetervisa (Domin) Hubbard	1
B. pubigera (Roem. & Shult.) S. T. Blake	1
B. whiteana (Domin) Hubbard	4
Indian and Southeast Asian species	
B. burmanica Bor	4
B. kurzii (Hook. f.) A. Camus	1
B. nilagirica Bor	1
B. remota (Retz.) Haines	1
B. semiverticillata (Rottl.) Alst.	1
B. tanimbarensis Ohwi	Ungrouped

Chapter 2

Natural Variation in *Brachiaria* and Existing Germplasm Collections

G. Keller-Grein,* B. L. Maass,* and J. Hanson**

Abstract

Seven perennial species of African origin—*Brachiaria arrecta*, *B. brizantha*, *B. decumbens*, *B. dictyoneura*, *B. humidicola*, *B. mutica*, and *B. ruziziensis*—have been used as fodder plants, particularly in tropical America. The history of the commercial cultivars is given, and their most important attributes are described. Access to germplasm diversity is essential for plant cultivar development. The world's major ex situ collections of *Brachiaria* germplasm are listed, together with descriptions of their holdings and management. The biogeographic origin of major species and the natural variation in terms of morphology and isozymes are described. Needs for future collection and conservation are identified.

Introduction

The genus *Brachiaria*, tribe Paniceae, includes about 100 species, which occur in the tropical and subtropical regions of both eastern and western hemispheres, but mostly in Africa (Renvoize et al., Ch. 1, this volume). Seven perennial species of African origin—*B. arrecta*, *B. brizantha*, *B. decumbens*, *B. dictyoneura*[1], *B. humidicola*, *B. mutica*, and *B. ruziziensis*—have been used as fodder plants, particularly in tropical America (Argel and Keller-Grein, Ch. 14, this volume; Pizarro et al., Ch. 15, this volume), and less so in Asia, the South Pacific, and Australia (Stür et al., Ch. 17, this volume). The limited commercial use of *Brachiaria* in Africa is because other forages are more appropriate to the prevailing livestock production systems (Ndikumana and Leeuw, Ch. 16, this volume). In addition, two annual species are of agricultural value as minor cereals—*B. deflexa* in West Africa (Wanous, 1990) and *B. ramosa* in India (A. Seetharam, 1994, personal communication).

Some African species, such as *B. plantaginea* and probably *B. mutica*, were introduced to the Americas during the early colonial period (Parsons, 1972; Sendulsky, 1978), probably unintentionally, as bedding material on slave ships. *Brachiaria decumbens* was introduced into Brazil in 1952, *B. brizantha* in 1965 (Sendulsky, 1978), and *B. ruziziensis* also in the 1960s. More recent introductions are *B. humidicola* and a material initially identified as *B. dictyoneura*, but now classified as *B. humidicola* (Renvoize et al., Ch. 1, this volume). *Brachiaria* is now the most widely used tropical grass genus, especially in Central and South America. In Brazil alone, about 40 million hectares of *Brachiaria* pastures exist, more than 85% of which consist of *B. decumbens* cv. Basilisk and *B. brizantha* cv. Marandu (Valle and Miles, 1994). However, there are certain constraints to the productivity of commercial cultivars, the most important being susceptibility to spittlebugs (Homoptera:Cercopidae), particularly in *B. decumbens* and *B. ruziziensis* (Valério et al., Ch. 6, this volume).

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1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Germplasm of *Brachiaria* has been collected since the 1950s, but the first comprehensive collecting mission for this genus was carried out only in the mid-1980s in eastern Africa, leading to the acquisition of a very large and diverse collection.

This chapter gives an inventory of the world's major ex situ collections of *Brachiaria* germplasm and outlines their management, and the biogeographic origin of major species and their natural variation in terms of morphology and isozymes.

Commercial Cultivars of *Brachiaria*

Brachiaria pastures rely essentially on a few widespread genotypes of seven species (Table 1). Five accessions of four species have been the source of 20 cultivars, released in different tropical American countries (Table 2). Consequently, the genetic base of cultivated *Brachiaria* is extremely.

Brachiaria decumbens cv. Basilisk

Probably the best known and most widely used *Brachiaria* cultivar is *B. decumbens* cv. Basilisk (signalgrass). It derives from seed (CPI 1694) introduced into Australia from the Ugandan Department of Agriculture in 1930. It was approved for commercial release in Australia in 1966 and registered in 1973 (Oram, 1990; Stür et al., Ch. 17, this volume). This cultivar is well adapted to infertile acid soils, and forms an

Table 1. Widely cultivated species and accessions of *Brachiaria*.

Species	Cultivar	Origin[a]	Institution and accession no.[b]				
			BRA-	CPI	CIAT	ILCA	Other and synonyms[c]
B. arrecta (syn. *B. radicans*)		exCOL[d]			6020[e]		
B. brizantha	Marandu	ZWE	000591	81408	6294	16550	IRI 822[e]; CIAT 6297, CIAT 6378, CIAT 6780; CPAC 3099, CPAC 3132; GC 127/78, GC 142/80; GO 023; CPATU 20, CPATU 78071; BRA-001554; CPI 118938
B. decumbens	Basilisk	UGA	001058	1694[e]	606	10871	GC 141/79
B. dictyoneura	Llanero	ZMB	001449	59610[e]	6133	12470	CPAC 3139; GC 769/86; CPI 118939
B. humidicola	Tully	exZAF[d]	001627	16707[e]	679	-	CPI 34679
B. mutica		Africa?			6047	6964?	FAO 43.456[e]
B. ruziziensis	Kennedy	RWA	000281	30623[e]	605	16692	K5832; GL 569/76, GL 579/76; GC 432/83, GC 433/83; CIAT 6714; BRA-002046

a. COL = Colombia; RWA = Rwanda; UGA = Uganda; ZAF = South Africa; ZMB = Zambia; ZWE = Zimbabwe.

b. Germplasm numbering systems: BRA = Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA); CPI = Commonwealth Scientific and Industrial Research Organisation (CSIRO); ILCA = International Livestock Centre for Africa.

c. Other germplasm numbering systems: CPAC = Centro de Pesquisa Agropecuária dos Cerrados; CPATU = Centro de Pesquisa Agropecuária do Trópico Úmido; FAO = Food and Agriculture Organization of the United Nations; GC = CNPGC; GL = Centro Nacional de Pesquisa de Gado de Leite (CNPGL); GO = Empresa Goiana de Pesquisa Agropecuária (EMGOPA); IRI = Instituto de Pesquisas IRI; K = Kitale Research Station.

d. ex = country of provenance of the accession, which may differ from that of its origin.

e. First number of those presented.

SOURCES: CSIRO, 1973; Nunes et al., 1984; Shenkoru et al., 1991; CIAT, tropical forages passport database; J. Hanson, unpublished data; C. B. do Valle, 1995, personal communication; J. F. M. Valls, 1995, personal communication.

Table 2. *Brachiaria* cultivars derived from accessions maintained in the germplasm bank held at CIAT, evaluated by the International Network for the Evaluation of Tropical Pastures (RIEPT), and released in tropical America.

Species cultivar name	CIAT accession no.	Release			Cultivar name	Reference
		Country	Institution[a]	Year		
B. brizantha						
IRI-822	6294	Brazil	CNPGC/EMBRAPA	1984	Marandu[b]	Nunes et al., 1984
		Cuba	IIPF	1987	Brizantha	J. J. Paretas, 1987, personal communic.
		Mexico	INIFAP	1989	Insurgente	Peralta M., 1990
		Venezuela	FONAIAP	1989	Gigante	AGROSSCA, 1989
		Costa Rica	MAG	1991	Diamantes 1	MAG, 1991
	26646	Colombia	ICA	1987	La Libertad[b]	Cuesta Muñoz and Pérez Bonna, 1987
B. decumbens						
cv. Basilisk	606	Cuba	IIPF	1987	Brachiaria	J. J. Paretas, 1987, personal communic.
		Mexico	INIFAP	1989	Chontalpo	Amaya H., 1990; Izquierdo Torres, 1984
		Panama	IDIAP	1989	Señal	Urriola et al., 1987
		Venezuela	FONAIAP	1989	Barrera[c]	AGROSSCA, 1989; Guenni et al., 1987
		Costa Rica	MAG	1991	Peludo	Lobo di Palma et al., 1991
B. dictyoneura						
CPI-59610	6133	Colombia	ICA	1987	Llanero	ICA, 1987
		Panama	IDIAP	1992	Gualaca	Montenegro and Pinzón, 1992
		Venezuela	FONAIAP	1992	Ganadero	Flores et al., 1992
		Costa Rica	MAG	1994	Brunca	Chi Chan et al., 1994
B. humidicola						
cv. Tully	679	Ecuador	INIAP	1983	INIAP-NAPO-701[b]	Muñoz M., 1985
		Panama	IDIAP	1989	Humidícola	Urriola, 1987
		Venezuela	FONAIAP	1989	Aguja	AGROSSCA, 1989
		Mexico	INIFAP	1992	Chetumal	Pastrana A. et al., 1992
		Colombia	ICA	1992	Humidícola	Pérez Bonna and Lascano, 1992

a. FONAIAP = Fondo Nacional de Investigaciones Agropecuarias, Venezuela; ICA = Instituto Colombiano Agropecuario; IDIAP = Instituto de Investigación Agropecuaria de Panamá; IIPF = Instituto de Investigaciones de Pastos y Forrajes, Cuba; INIAP = Instituto Nacional de Investigación Agropecuaria, Ecuador; INIFAP = Instituto Nacional de Investigaciones Forestales y Agropecuarias, Mexico; MAG = Ministerio de Agricultura y Ganadería, Costa Rica.

b. These cultivars were developed by the institution indicated and released in the respective country before they were distributed by CIAT through the RIEPT.

c. Also known as "pasto alambre" (wire grass).

aggressive, high-yielding sward that withstands heavy grazing and trampling. It is a palatable grass of good forage quality and gives good animal performance. However, its susceptibility to spittlebugs reduces its value as a pasture plant in areas where this pest is a major constraint, for example, in the neotropical savannas (Lapointe, 1993; Valério et al., Ch. 6, this volume). Signalgrass can also cause photosensitization in livestock (Lascano and Euclides, Ch. 7, this volume).

Brachiaria brizantha cv. Marandu

Brachiaria brizantha cv. Marandu (IRI 822; BRA-000591), released in 1984 in Brazil by EMBRAPA, originates from germplasm introduced to the Ibirarema region, São Paulo, Brazil, from the Zimbabwe Grasslands Research Station, Marandella (now Marondera) (Nunes et al., 1984). Its antibiotic resistance to spittlebugs (Ferrufino and Lapointe, 1989) has led to the rapid adoption of

cv. Marandu throughout the American tropics. This grass provides a palatable forage of nutritional quality similar to that of *B. decumbens* cv. Basilisk. However, cv. Marandu does not tolerate poor soil drainage and requires higher soil fertility than cv. Basilisk; thus, it does not persist on the low-fertility Ultisols and Oxisols that are widespread in tropical America. In mixed pastures, this cultivar seems to exert an allelopathic effect on several legume species (Rodrigues and Reis, 1994).

Brachiaria ruziziensis cv. Kennedy

Brachiaria ruziziensis, native to the Ruzi Valley in Zaire and Burundi, is widely distributed in tropical countries. It is known as ruzigrass or Congo signalgrass. Seed originally obtained from the Institut national pour l'étude agronomique du Congo Belge (INEAC) at Rubona, Rwanda, was multiplied at the Kitale Research Station, Kenya, in the early 1960s (Barnard, 1969; Boonman, 1993), and spread to various sites in continental Africa and Madagascar. The material grown in Australia (CPI 30623) originates from seed received from the Agronomy Station of Lac Alastra, Madagascar, in 1961, and was released under the common name ruzigrass by the Queensland Herbage Plant Liaison Committee in 1966 (Barnard, 1969). It is also known as cv. Kennedy (Skerman and Riveros, 1990), although this name does not appear in the release notice. The same germplasm is probably cultivated in the Americas.

Ruzigrass provides palatable forage of high nutritive quality. It seeds freely, but requires fertile, well-drained soils; it is also highly susceptible to spittlebugs and less productive than *B. decumbens*. In Australia, ruzigrass was supplanted by *B. decumbens* cv. Basilisk, once seed of this cultivar became readily available (W. W. Stür, 1994, personal communication).

Brachiaria humidicola cv. Tully

Brachiaria humidicola was introduced into Australia as CPI 16707 from Rietondale Experiment Station, Pretoria, South Africa, by J. F. Miles in 1952 (Oram, 1990). Samples went from Australia to Fiji and Papua New Guinea, from where identical material was reintroduced to the Tully area of northern Queensland in 1973; cv. Tully (also known as koroniviagrass) is derived from this. It was approved for commercial release in 1980 and registered in 1981 (Oram, 1990). The material cultivated in tropical America (CIAT 679) probably represents the same genotype. This cultivar is an aggressive grass that forms a dense sward and suppresses weeds. It tolerates heavy grazing and shade, and is adapted to poorly drained and infertile acid soils. Its strongly stoloniferous growth habit makes *B. humidicola* valuable as a ground cover in tree plantations and for erosion control, but is not compatible with twining legumes. Forage quality is lower than that of *B. brizantha*, *B. decumbens*, and *B. ruziziensis*, and seed production is limited at low latitudes. *Brachiaria humidicola* is tolerant of, but is not truly resistant to, spittlebugs (Lapointe, 1993) and has shown susceptibility to rust caused by *Uromyces setariae-italicae* in tropical America (Parra Orozco, 1992).

Brachiaria dictyoneura cv. Llanero

Some doubt exists over the taxonomic identification of this cultivar, which Renvoize reclassified as a form of *B. humidicola* (Renvoize et al., Ch. 1, this volume).

Cultivar Llanero was released in Colombia by the Instituto Colombiano Agropecuario (ICA) in 1987 (ICA, 1987). It derives from seed (CPI 59610) introduced from the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) in 1978 as CIAT 6133 and was originally collected by R. W. Strickland in Zambia in 1971. Cultivar Llanero is well adapted to low-fertility acid soils, provided they are well drained. Its nutritive value is moderate, but higher than that of commercial *B. humidicola*. Seed

dormancy causes considerable problems in the determination of physiological seed quality and field emergence of seeds (Hopkinson et al., Ch. 8, this volume). Like *B. humidicola*, cv. Llanero is tolerant of, but is not resistant to, spittlebugs, and has proven to be an excellent host for spittlebug nymphs (Ferrufino and Lapointe, 1989).

Brachiaria mutica and *B. arrecta* (syn. *B. radicans*)

Although no commercial cultivars of *B. mutica* or *B. arrecta* are registered, both species, especially the former, are widely distributed in the tropics and well known under their common names: paragrass and tannergrass, respectively. They are closely related and are distinguished from each other only by the arrangement of spikelets, which are usually paired or clustered on the rachis in *B. mutica* and single in *B. arrecta* (Clayton and Renvoize, 1982). The cultivated material of both grasses appears uniform, and is commonly vegetatively propagated. Both species are so well adapted to swampy and seasonally flooded conditions that they are ranked among the best grasses for such locations in the tropics, particularly *B. mutica*, which is frequently used as forage in ponded pastures in drier areas of Australia. However, paragrass can become a weed in irrigation ditches and drains. In Australia, it is susceptible to a leafhopper, which can severely reduce pasture productivity (Schultze-Kraft and Teitzel, 1992; Stür et al., Ch. 17, this volume). Nitrate toxicity has been reported in cattle grazing tannergrass (Lascano and Euclides, Ch. 7, this volume).

Genetic Resources of *Brachiaria*

Germplasm collection

In the 1950s, A. V. Bogdan of the National Agricultural Research Station at Kitale, Kenya, collected 154 *Brachiaria* accessions, emphasizing *B. brizantha* and *B. ruziziensis* (J. K. Kemei, 1994, personal communication). Some materials were exchanged with other African institutions. A few accessions from this collection were incorporated into the large overseas collections of the United States Department of Agriculture (USDA) or CSIRO.

In the 1960s and mid-1970s, Brazilian institutions, such as the Instituto de Pesquisas IRI (IRI) at Matão, the Centro de Pesquisa Agropecuária do Trópico Úmido (CPATU) in Belém, and the Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG) in Belo Horizonte, held small working collections of 10 to 30 accessions each, which they exchanged among themselves (Shock et al., 1979; CPATU, unpublished germplasm list; EPAMIG, unpublished germplasm catalog).

During the 1970s, the CSIRO collected *B. brizantha* accessions in Zimbabwe (then Rhodesia) and Zambia (Staples, 1971), and about 30 accessions of different species from eastern, central, and southern Africa (Strickland, 1972). *Brachiaria* germplasm was also collected by A. J. Oakes and E. C. Bashaw of the USDA (USDA, 1974; 1978). Both the CSIRO and USDA missions aimed at collecting a wide range of grasses and legumes, and placed no particular emphasis on *Brachiaria*.

Between 1974 and 1984, about 220 *Brachiaria* accessions, particularly of *B. brizantha, B. decumbens*, and *B. jubata*, were collected by the former Trust Fund Forage Collection and Evaluation Project of the Food and Agriculture Organization of the United Nations (FAO), based at the National Agriculture Research Station at Kitale (Ibrahim, 1984; J. K. Kemei, 1994, personal communication). Part of this collection was sent to CIAT in 1981; however, seed viability was so low that most accessions were lost.

Other collections, for example, that of Cuba, comprise mainly material donated by other institutions, including the CSIRO, CIAT, IRI, and CPATU

(EEPFIH, 1988). Hence, a few germplasm accessions are very widely distributed and have probably been unknowingly duplicated in the same institution.

Until the mid-1980s, no more than 150 distinct and viable accessions of the genus *Brachiaria* existed in the major collections of tropical forage germplasm. As of June 1984, only 76 accessions of nine *Brachiaria* species were available in the CIAT gene bank in Colombia. This narrow germplasm base and the above-mentioned limitations of existing *Brachiaria* cultivars motivated CIAT to broaden the genetic base of its *Brachiaria* holdings through direct collection. Collaborators were the International Livestock Centre for Africa (ILCA) and several African institutions. The 1984/85 expedition in eastern Africa was supported by the International Board for Plant Genetic Resources (IBPGR) and led by G. Keller-Grein and collaborators. About 800 accessions of at least 23 known species were collected, thus increasing, by more than 10 times, the *Brachiaria* germplasm collection held at CIAT (Mengistu, 1985a; 1985b; 1986; G. Keller-Grein, unpublished data).

Further collection has been carried out by ILCA and by IBPGR-funded missions. H. Moss of IBPGR collected 32 seed samples in southern Africa; these are stored in the gene bank of the Royal Botanic Gardens, Kew, UK (W. G. Ayad, 1994, personal communication).

The Roodeplaat Grassland Institute, Pretoria, South Africa, collected 46 accessions of *B. nigropedata* and other *Brachiaria* species in the Kruger National Park, South Africa (M. Jooste, 1994, personal communication).

Existing collections and their management

Four major and three minor collections of *Brachiaria* exist ex situ (Table 3), holding a total of 987 distinct accessions of 33 known species. About 40% of existing accessions are of *B. brizantha*, and another 39% are of *B. humidicola*, *B. decumbens*, *B. nigropedata*, *B. jubata*, or *B. ruziziensis*.

To minimize genetic drift, shift, or erosion, proper maintenance of germplasm is essential. But conservation of *Brachiaria* germplasm as seed is extremely difficult because of problems in seed production and processing (Hopkinson et al., Ch. 8, this volume). Hence, most major genetic resource centers maintain live field collections.

Because most *Brachiaria* species are apomicts, problems of contamination of accessions by outcrossing during rejuvenation are limited. Current practices to avoid mechanical mixtures are adequate. Sexually reproducing biotypes would be better conserved in vitro; however, no conservation method has yet been developed for this.

CIAT. The *Brachiaria* collection maintained at CIAT comprises nearly 700 accessions of 27 identified species. More than 80% of the collection was obtained during the 1984/85 expedition; the remainder corresponds to donations, mainly from Australia, USA, and Kenya.

Almost 50% of the accessions are of *B. brizantha*, reflecting in part its wide distribution and in part the focus on this species as a promising pasture grass. Accessions of the closely related *B. decumbens* and *B. ruziziensis* account for only 15% of the collection. This reflects their narrow natural distribution. Other well-represented species are *B. humidicola* (11%), *B. jubata* (8%), and *B. nigropedata* (5%).

The collection maintained at CIAT is used to develop cultivars through selection or breeding. A large part of it has been tested at CIAT's major screening sites in Colombia, Brazil, Peru, and Costa Rica (Argel and Keller-Grein, Ch. 14, this volume; Pizarro et al., Ch. 15, this volume). Promising accessions are

Table 3. Genetic resources of *Brachiaria* conserved in major world collections, as of May 1994.

Species	Accessions conserved[a]							
	CIAT	ILCA	CENARGEN[b]	ATFGRC	USDA	GBK	RGI/ARC	Total[b]
B. arrecta	6	-	5	1	-	-	-	7
B. bovonei	5	7	3	-	-	-	-	9
B. brizantha	330	263	241	52	23	15	1	399
B. comata	5	1	-	-	-	-	-	6
B. decumbens	62	56	54	13	8	10	1	83
B. deflexa	10	-	1	2	1	3	-	13
B. dictyoneura	9	7	3	5	5	-	3	17
B. eminii	1	-	-	4	-	-	-	5
B. eruciformis	9	12	-	-	5	-	-	26
B. fasciculata	-	-	-	-	10	-	-	10
B. humidicola	78	49	60	10	11	1	-	105
B. jubata	54	49	41	1	-	5	-	55
B. lachnantha	2	6	-	-	-	-	-	6
B. nigropedata	32	19	1	19	5	-	26	80
B. plantaginea	2	-	-	1	3	-	-	5
B. platynota	11	16	2	2	-	1	-	18
B. ramosa	1	-	-	-	4	-	-	5
B. ruziziensis	45	23	20	30	5	7	1	57
B. serrata	6	7	5	-	1	-	5	16
B. subulifolia	5	5	5	-	-	-	-	9
B. xantholeuca	3	-	-	2	2	-	-	7
Other species[c]	9	-	1	12	2	2	-	22
Not identified	2	-	1	19	5	7	2	27
Total	687	520	443	174	90	51	39	987

a. ATFGRC = Australian Tropical Forage Genetic Resources Centre of CSIRO, Australia; CENARGEN = Centro Nacional de Recursos Genéticos e Biotecnologia of EMBRAPA, Brazil; GBK = Genebank of Kenya; ILCA = International Livestock Centre for Africa, Ethiopia; RGI/ARC = Roodeplaat Grassland Institute of the African Research Council, South Africa; USDA = United States Department of Agriculture.

b. Estimated numbers of distinct accessions.

c. Species with fewer than five accessions: *B. advena*, *B. dura*, *B. lata*, *B. leersioides*, *B. mutica*, *B. oligobrachiata* (syn. *B. platytaenia*), *B. reptans*, *B. semiundulata*, *B. serrifolia*, *B. subquadripara*, *B. umbratilis*, *B. villosa*.

SOURCES: CIAT tropical forage germplasm passport database; J. Hanson, ILCA, unpublished data; B. C. Pengelly and B. Thomas, CSIRO, 1994, personal communication; G. R. Lovell, ARS/USDA, 1994, personal communication; J. K. Kemei, GBK, 1994, personal communication; M. Erasmus and M. Jooste, RGI/ARC, 1994, personal communication.

distributed through forage evaluation networks to national programs: the International Network for the Evaluation of Tropical Pastures (RIEPT, its Spanish acronym) in the American tropics; the Southeast Asian Forage Research and Development Network (SEAFRAD) in Asia; and the West and Central African Feed Resources Network (RABAOC, its French acronym) in sub-Saharan Africa.

Important ongoing activities are assessment of reproductive mode (Valle and Savidan, Ch. 10, this volume) and screening for resistance to spittlebugs (Valério et al., Ch. 6, this volume). Computerized information on the collection is available, and a catalog of *Brachiaria* and other forage germplasm from Africa is in preparation (G. Keller-Grein and B. L. Maass, unpublished data).

The main part of the *Brachiaria* germplasm at CIAT is maintained in a field collection at Santander de Quilichao in the Colombian Department of Cauca (3°06' N; 990 m.a.s.l.; 1,845 mm annual rainfall; Oxisol, 89% Al saturation, pH 4.0). Part of the collection has been transferred to a higher altitude site near Popayán (1,800 m.a.s.l.; 2,000 mm annual rainfall; volcanic soil, pH 5.5). The quality and quantity of seed produced at Popayán are superior to those produced at Quilichao (A. Ortiz, 1994, personal

communication). Seed is stored in the active collection at 5-10 °C, and in the base collection at -20 °C in the gene bank at CIAT headquarters.

ILCA. At ILCA is the second largest *Brachiaria* collection (522 accessions), originating almost entirely from the CIAT-ILCA expedition in 1984/85. Thus, it largely duplicates the collection maintained at CIAT. Accessions of *B. brizantha* account for half of the collection.

Morphological classification and agronomic evaluation of about 300 accessions have been conducted at Zwai, Ethiopia (Heering, 1987). Information on the collection has been computerized, and passport data were published in a germplasm catalog (Shenkoru et al., 1991).

Wherever possible, the germplasm is maintained in the gene bank at ILCA headquarters, where seed is dried to 5% moisture content, packed in laminated, aluminum-foil bags, and stored in the active gene bank at 8 °C and in the base gene bank at -20 °C. However, some accessions produce little viable seed. Thus, a live field collection of most accessions is also maintained at Zwai in the Ethiopian Rift Valley (8° N; 1,650 m.a.s.l.; 500-600 mm annual rainfall; pH 8.0).

CENARGEN/EMBRAPA. Of a total collection of almost 450 accessions held at the Centro Nacional de Recursos Genéticos e Biotecnologia (CENARGEN), about 80% originated from the CIAT-ILCA African collection. This is an active collection that has been acquired for selection of superior material out of the natural variation. Morphological characterization of 312 accessions of 13 species was conducted at Campo Grande, Brazil (Valle et al., 1993b), herbarium specimens were taken, and species identity was confirmed (C. B. do Valle, 1995, personal communication). The determination of reproductive mode was complemented by studies of those accessions that had not been previously determined at CIAT (Valle and Savidan, Ch. 10, this volume). Spittlebug resistance was assessed at Campo Grande (Valério et al., Ch. 6, this volume). The agronomic performance of a relatively large collection of new *Brachiaria* germplasm was assessed at Planaltina (Pizarro et al., Ch. 15, this volume), and also at Campo Grande (Valle et al., 1993a).

ATFGRC/CSIRO. Almost the entire collection held at the Australian Tropical Forage Genetic Resource Centre (ATFGRC) was obtained through CSIRO expeditions in Africa (Staples, 1971; Strickland, 1972; B. C. Pengelly and B. Thomas, 1994, personal communication). Of the 177 accessions, 70% are *B. brizantha*, *B. decumbens*, *B. humidicola*, *B. nigropedata*, or *B. ruziziensis*. Duplicates of a major part of the collection are held at CIAT and other institutions. Passport information on the collection is computerized and was published in the Australian Plant Introduction Review (e.g., CSIRO, 1973).

The *Brachiaria* collection held by ATFGRC/CSIRO is maintained as seed under long-term storage in the gene bank at Samford, near Brisbane, Australia. Germplasm has been distributed as seed.

USDA. Most of the germplasm maintained by the USDA was collected incidentally during expeditions focused on other genera; some was obtained through donations from other collections. About 60% of the 90 accessions belong to *B. brizantha*, *B. decumbens*, *B. fasciculata*, or *B. humidicola*. Twelve additional species are also represented. Passport data are fully computerized.

Part of the USDA collection is maintained in the field at Griffin, Georgia, and part as seed at Beltsville, Maryland. Several accessions have been lost because of low viability of the original seeds (G. R. Lovell, 1994, personal communication). Germplasm is distributed as seed only.

GBK. The Genebank of Kenya (GBK) acquired all seed samples from the collections of A. V. Bogdan, K. M. Ibrahim, and collaborators after the completion of the FAO project at Kitale in 1989. The surviving accessions had only 5%-25% viability, and almost half of the collection (202 accessions) had died (J. K. Kemei, 1994, personal communication). Regenerated seed of about 30 accessions is now stored at -20 °C, and the GBK has again collected from some of the original sites. *Brachiaria brizantha* and *B. decumbens* account for half of the 51 accessions comprising this collection; a few accessions each of several other species make up the other half.

RGI/ARC. The collection at the Roodeplaat Grassland Institute (RGI) of the African Research Council (ARC) comprises 39 accessions, 67% of which belong to *B. nigropedata*. Most of the *B. nigropedata* accessions were obtained through direct collection conducted mainly in the Kruger National Park. *Brachiaria nigropedata* grows on soils of granitic origin and is considered a valuable component of natural grasslands in southern Africa; collections were made to investigate its agricultural potential (M. Erasmus and M. Jooste, 1994, personal communication). Many of the accessions are duplicated at CSIRO, Australia, and some have been sent to Argentina (M. Erasmus and M. Jooste, 1994, personal communication).

Computerized information on the collection is available.

The collection at RGI/ARC is maintained primarily as seed. One accession of *B. ruziziensis*, which does not produce seed, is maintained vegetatively. Germplasm has been distributed as seed (M. Jooste, 1994, personal communication).

Germplasm distribution

The low levels of seed production in *Brachiaria* are a constraint to the dissemination of germplasm. Distributing vegetative material is not advisable, because of phytosanitary risks.

To facilitate germplasm transfer, CIAT and ILCA developed techniques for in vitro culture of axillary buds (CIAT, 1986). The success rate in culture and the amount of contamination and necrosis differed among accessions and species; *B. jubata*, *B. humidicola*, and *B. platynota* were the most intractable species (Table 4). Only uncontaminated cultures were distributed.

A large portion of the *Brachiaria* germplasm collected by CIAT and ILCA in Africa was transferred to Colombia by in vitro culture. Germplasm was subsequently distributed to screening sites in Brazil, Peru, and Costa Rica in the form of in vitro cultures.

Table 4. In vitro cultures of *Brachiaria* species at the International Livestock Centre for Africa (ILCA).

Species	Accessions cultured (no.)	Total cultures (no.)	Clean cultures[a] (%)	Necrotic cultures (%)
B. bovonei	1	13	23	46
B. brizantha	36	885	24	45
B. decumbens	3	80	69	9
B. humidicola	4	51	2	51
B. jubata	7	69	0	83
B. lachnantha	3	65	34	55
B. platynota	2	20	0	60

a. That is, suitable for distribution.

SOURCE: J. Hanson, unpublished data.

Biogeography and natural distribution of major species

Table 5 summarizes the geographic, climatic, and edaphic characteristics of collecting sites of seven *Brachiaria* species, native to Africa, that are considered important for tropical pasture development or are represented by a large number of accessions in germplasm collections. Maps (Appendix) show the natural distribution of the species and germplasm collection sites, thus highlighting geographical gaps in the ex situ collections.

Brachiaria brizantha (Map 1) is widespread in tropical Africa, occurring in open and wooded grasslands, along margins of woodlands and thickets, and in upland grasslands. The collection sites of available germplasm cover the natural geographic range in eastern and southeastern Africa. However, a considerable collecting gap exists for West Africa and southern tropical Africa (especially Zaire and Zambia), which form centers of diversity for this species (S. A. Renvoize, 1993, unpublished report).

Brachiaria decumbens, in contrast to the closely related *B. brizantha*, has a narrow natural distribution (Map 2). Western Kenya, Rwanda, and Burundi are well covered by germplasm holdings. However, except for cv. Basilisk, no germplasm is available from Uganda, where the species is very common and where numerous herbarium specimens were collected. In addition, no germplasm has been collected from western Tanzania or Zaire, where the species also occurs naturally. It is found in deciduous bushland, grasslands, and at forest edges.

Brachiaria ruziziensis also has a narrow natural distribution (Map 3). Germplasm collections were made from Burundi and Rwanda, but none from Zaire. The grass occurs in grasslands and disturbed places.

The existing germplasm collections represent the natural distribution of *B. humidicola* (Map 4) in eastern and southeastern Africa, but gaps exist for Nigeria, Sudan, and southern Africa. The usual habitat comprises seasonally swampy grasslands.

Considering the natural distribution of *B. dictyoneura* (Map 5), no germplasm material is available from Sudan, Uganda, northern and western Tanzania, Zambia, or Mozambique.

Brachiaria jubata (Map 6), widely distributed in tropical Africa, occurs in seasonally moist grasslands, wet bushland, and at margins of swamps. Although the available germplasm

Table 5. Geographic, climatic, and edaphic characteristics of collecting sites of seven *Brachiaria* species in ex situ germplasm.

Species	Accessions (no.)	Latitude	Altitude (m.a.s.l.)	Annual rainfall (mm)	Dry months[a] (no.)	Soil pH
B. brizantha	420	25°05'S-12°36' N	80-2310	590-2770	0-7	4.0-8.0
B. decumbens	75	4°21'S- 1°09' N	840-2290	870-1900	0-5	4.9-7.0
B. dictyoneura	15	25°23'S- 5°58' N	200-2000	680-1320	2-8	5.5-7.0
B. humidicola	90	20°17'S-11°21' N	560-2375	600-2800	2-7	4.0-7.0
B. jubata	60	18°44'S- 9°41' N	220-2460	630-1900	0-7	4.5-7.8
B. nigropedata	70	25°36'S-16°20' S	190-1570	590-1110	7	4.6-7.4
B. ruziziensis	50	4°05'S- 2°54' S	590-1940	890-1710	3-4	5.0-6.8

a. Rainfall is <65 mm per month.

SOURCES: See sources for Table 3.

collection includes a substantial number of accessions, areas from which they were collected do not adequately represent the natural distribution of this species: except for three collections from Togo and Cameroon; no germplasm is available from western and central Africa. Several regions in eastern and southeastern Africa (e.g., Uganda, Malawi, Zambia) are not represented in ex situ germplasm collections, and there is no germplasm from Angola.

The germplasm collection of *B. nigropedata* (Map 7) does not adequately represent its natural distribution in southern and eastern Africa. In Zimbabwe, germplasm collected from different sites, usually dry sandy soils in open or wooded grasslands, is highly uniform morphologically. Obtaining germplasm from other regions may introduce more variability.

Recommendations for future collection

Species. Some species with agronomic potential are inadequately represented in existing collections; for example, only 15 accessions of true *B. dictyoneura* exist. In the wild, this species shows some variation in robustness, and large variation in leaf-blade width and raceme number (S. A. Renvoize, 1993, unpublished report); however, leaf-blade width in accessions at CIAT ranges only from 7 to 11 mm, and the upper range, from 11 to 30 mm, is not represented. Similarly, the number of racemes in accessions at CIAT ranges from 3 to 8; but except for CIAT 16191, which has 11 racemes, no accession represents the upper end of variation: 10 to 14 racemes (S. A. Renvoize, 1993, unpublished report).

Brachiaria jubata is a common species, widely distributed in western and eastern Africa. It has long, leafy culms and considerable grazing value (Rose Innes and Clayton, 1977; S. A. Renvoize, 1993, unpublished report), particularly in poorly drained, wet soils. The known upper range of leaf-blade width (extending to 17 mm) is not represented in existing collections (S. A. Renvoize, 1993, unpublished report). Thus, new genotypes with higher forage potential may still be obtained in the wild.

Brachiaria mutica is a widely used, good-quality forage grass for swampy and seasonally waterlogged areas. Only five morphologically uniform accessions exist in the major collections. Varietal differences have been observed in Thailand and Burma (Schultze-Kraft and Teitzel, 1992); these need to be represented in the collections. West Africa, where this species is widely distributed, also holds considerable potential for providing more variability. Similarly, *B. arrecta* is represented by only six morphologically very similar accessions in existing ex situ collections.

Brachiaria decumbens and *B. brizantha* are predominantly apomictic species; however, sexuality has been found in both, and further collecting to seek new sexual germplasm would be worthwhile. For example, many accessions of *B. decumbens* collected in Rwanda and three accessions collected close to the Ugandan border, west of Kisumu, Kenya, are sexual (Valle, 1990; B. L. Maass, unpublished data).

The agronomic potential of several other species should be explored. *Brachiaria subquadripara*, a creeping, stoloniferous, and highly shade-tolerant perennial (but is sometimes reported as an annual), is valuable for pastures and ground cover in tree plantations in Southeast Asia (Schultze-Kraft, 1992). However, only four accessions exist in the major *Brachiaria* germplasm collections. To broaden this species's germplasm base, it may be worth exploring such areas of tropical Asia as India, Sri Lanka, Burma, and Malaysia.

Brachiaria falcifera, although closely related to *B. jubata*, is distinguished by its caespitose habit; narrowly linear, partially folded leaf blades; and fewer racemes (S. A. Renvoize, 1993, unpublished report). It

is a dominant component of the typical fire-proclimax (peppercorn) tree savannas and much used for grazing on the Accra and Ho-Keta plains in Ghana (Rose Innes and Clayton, 1977). The species is adapted to frequent fires and an erratic bimodal pattern of rainfall (S. A. Renvoize, 1993, unpublished report). No accession of this species is conserved in major *Brachiaria* germplasm collections.

Brachiaria ambigens, a densely tufted perennial, native to East Africa, may have potential as a forage in semiarid grasslands (Ibrahim and Kabuye, 1987; C. H. S. Kabuye, 1994, personal communication). However, no germplasm of this species exists in ex situ collections.

Brachiaria dura, which is adapted to sandy soils of low fertility (Verboom, 1966), also may have potential as a forage for dry areas (Skerman and Riveros, 1990). The two accessions of this species available in the collection at CIAT show little promise: they have poor vigor and very narrow, convolute leaf blades.

The annual *B. distachya* is reported to have agronomic value in Southeast Asia, where it is used as a natural forage grass. According to Manidool (1992), it is highly palatable to livestock, and tolerates light shade and poor soils. It warrants more attention.

Genetic conservation. Rapidly increasing human population and an accelerated conversion of natural vegetation to cropland represent a serious threat to native plant genetic resources in most of East Africa and several areas of West Africa. Although most of the germplasm in existing *Brachiaria* collections is from eastern and southeastern Africa, some areas are still insufficiently sampled, such as Uganda; northern, western, and southern Tanzania. Some regions in Africa have not been sampled, such as Mozambique; and western, central, and southwestern Africa, including Zaire, Zambia, and Angola. A very few accessions of *B. brizantha* and *B. jubata* only have been collected from Cameroon and Togo.

Natural Variation in *Brachiaria* Germplasm

Most information about *Brachiaria* has been generated from one or few genotypes per species. Little attention was paid to natural variation because no large germplasm collections were available until recently.

Now, research on the genetic diversity of *Brachiaria* includes studies on morphology, phenology, agronomy, cytogenetics, reproductive biology, isozymes, and molecular markers, as well as physiological traits of adaptation, forage quality, and response to pests and diseases. Some characteristics are dealt with in other chapters of this volume, for example, reproductive mode (Valle and Savidan, Ch. 10), reaction to spittlebugs (Valério et al., Ch. 6), and forage quality (Lascano and Euclides, Ch. 7). In this chapter, we focus on morphological and isoenzymatic diversity.

Morphology

The genus *Brachiaria* is morphologically diverse, both among and within species. Interspecific variation in, for example, plant habit ranges from procumbent stoloniferous species (e.g., *B. arrecta*, *B. humidicola*, and *B. subquadripara*), through ascending forms (e.g., *B. ruziziensis*), to those erect accessions of *B. brizantha* that grow more than 2 m tall. Form and width of the rachis also differ among species: some have a triquetrous, extremely narrow (<1 mm) rachis (e.g., *B. brizantha*, *B. humidicola*, and *B. nigropedata*); and others, a broad (up to 4 mm), ribbon-like, subfoliaceous rachis (e.g., *B. ruziziensis* and *B. platynota*). Intraspecific variation appears to be particularly wide for *B. brizantha*, which contains decumbent, ascending, and erect growth habits.

Morphological characterization of 297 germplasm accessions of 10 species

has been conducted at the ILCA research station at Zwai, Ethiopia (Heering, 1987). Outside Africa, Valle et al. (1993b) recorded 25 morphological characters in 312 accessions of 13 species at Campo Grande, Brazil, and in 172 accessions of 12 species at Quilichao, Colombia. The morphological groups identified by principal component and cluster analyses at both sites had some similarities (Valle et al., 1993b).

The plant characteristics used for classification should be environmentally stable. A comparative study of morphological data on 88 accessions of *Brachiaria* evaluated at both Campo Grande and Quilichao showed high correlation coefficients for leaf width and length of the basal raceme of the inflorescence. But little correlation was found between the sites for length of inflorescence, number of racemes per inflorescence, and number of spikelets on the basal raceme (B. L. Maass and C. B. do Valle, unpublished data). Environmental stability for additional characters is being assessed.

The largest study of morphological variation to date was conducted in 1994 at the CIAT research station at Quilichao. A total of 37 morphological characters was recorded on 586 accessions of 15 species (G. Keller-Grein, unpublished data). Because data are still being analyzed, we describe here only the variation detected for a few selected morphological characteristics of the *B. brizantha/B. decumbens/B. ruziziensis* species complex.

As described previously by Valle et al. (1993b), the greatest morphological variation was registered for *B. brizantha*. Considerable variation for plant height and leaf length and width exists within the complex (Figure 1). For all characters, *B. brizantha* is the most variable of the three species, perhaps reflecting in part the larger number of accessions of this species, but probably also reflecting its greater inherent diversity.

When the ex situ germplasm collection at Quilichao was compared with

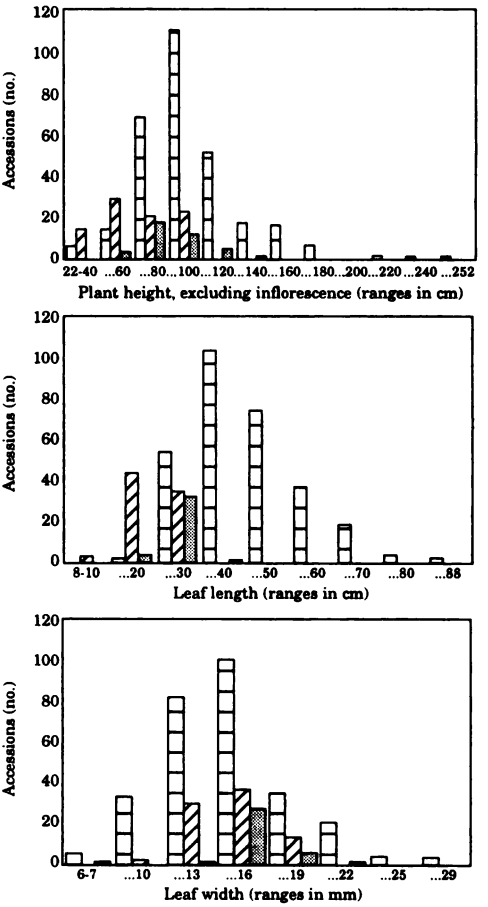

Figure 1. Variation in plant height and leaf length and width of *Brachiaria brizantha* (□), *B. decumbens* (▨), and *B. ruziziensis* (▩) in the collection maintained at CIAT (G. Keller-Grein, unpublished data).

the wild population (based on herbarium specimens held at the Royal Botanic Gardens, Kew, UK; S. A. Renvoize, 1993, unpublished report), the collected *B. brizantha* germplasm appeared to cover the range of morphological variation observed in the wild. A large proportion of the *B. decumbens* collection at Quilichao has relatively long leaf blades, falling in the intermediate range between *B. brizantha* and *B. decumbens*. The germplasm of *B. ruziziensis* represents the normal range of variation found in the species, except for one accession that had an exceptionally narrow rachis (S. A. Renvoize, 1993, unpublished report).

Isozymes

Isozyme polymorphisms provide environmentally stable markers that can be used to identify genotypes and true hybrids unequivocally and to quantify degree of relatedness among genotypes. Isozymes have been used for detecting hybrids in *Brachiaria* (Cruz et al., 1989; Hacker, 1988), where difficulty in achieving complete and opportune emasculation leaves the chance of accidental selfing. Particularly, a- and $-esterase (EST) isozyme bands are being used in CIAT's *Brachiaria* breeding program to verify the hybrid nature of F_1 progeny (Lapointe and Miles, 1992).

Isozymes determined by polyacrylamide gel electrophoresis (PAGE) were studied for analysis of genetic variation of a large portion of the germplasm collection maintained at Quilichao, with emphasis on the species complexes of *B. brizantha/B. decumbens/ B. ruziziensis* (containing 340 accessions) and *B. dictyoneura/B. humidicola* (76 accessions) (C. M. Meghji and B. L. Maass, unpublished data). Only five enzyme systems showed polymorphism (Table 6; Figure 2). In *Brachiaria*—unlike the legumes *Arachis* (Maass et al., 1993) and *Stylosanthes* (B. L. Maass and S. I. Marulanda, unpublished data)—GOT proved to be a highly polymorphic isozyme, discriminating 30% across all five species, while PRX discriminated 11% and DIA, 8% of the accessions (Table 7).

In the overall analysis of these three isozyme systems, 332 distinct patterns in 416 accessions led to a total discrimination of 80%, which demonstrates that large natural variability exists and is captured in this ex situ germplasm collection. The polymorphism in both a- and ß-EST isozymes is such that the analysis is concentrating only on major bands; it has not yet been completed.

Some species, however, can be easily distinguished by specific bands or banding patterns, such as *B. humidicola* and *B. ruziziensis* with α- and ß-EST. The almost complete absence of bands in PRX zymograms for *B. humidicola* and *B. jubata* samples appears to be a marker for those species, in conjunction with the unique DIA and EST zymograms found (Figure 2). The accession CIAT 6133, previously labeled as *B. dictyoneura*, also shows the typical *B. humidicola* DIA zymograms, which would support the taxonomic integration of this accession into the latter species (Renvoize et al., Ch. 1, this volume); however, it presents two bands in PRX, which only three other accessions of *B. humidicola* have: CIAT 16876, 26371, and 26570.

Table 6. Isozymes from leaf tissue used to fingerprint *Brachiaria* germplasm with polyacrylamide gel electrophoresis (PAGE), resolution of system, and polymorphism encountered.

Marker	EC number[a]	Resolution[b]	Polymorphism
ACP (α,ß-acid phosphatase)	3.1.3.2	+	-
ADH (alcohol dehydrogenase)	1.1.1.1	+	-
DIA (diaphorase)	1.6.99.-	+	+
α-EST (α-esterase)	3.1.1.-	+	+++
ß-EST (ß-esterase)	3.1.1.-	+	+++
GOT (glutamate oxaloacetate transaminase)	2.6.1.1	+	++
G6PDH (glucose-6-phosphate dehydrogenase)	1.1.1.49	-	-
MDH (malate dehydrogenase)	1.1.1.37	+	-
ME (malic enzyme)	1.1.1.40	-	-
PRX (peroxidase)	1.11.1.7	+	+
SKDH (shikimate dehydrogenase)	1.1.1.25	-	-

a. EC = Enzyme Commission.

b. Resolution of bands/polymorphism: +++ = very good/very high; + = acceptable/moderate; - = poor/none.

SOURCE: C. M. Meghji, unpublished data.

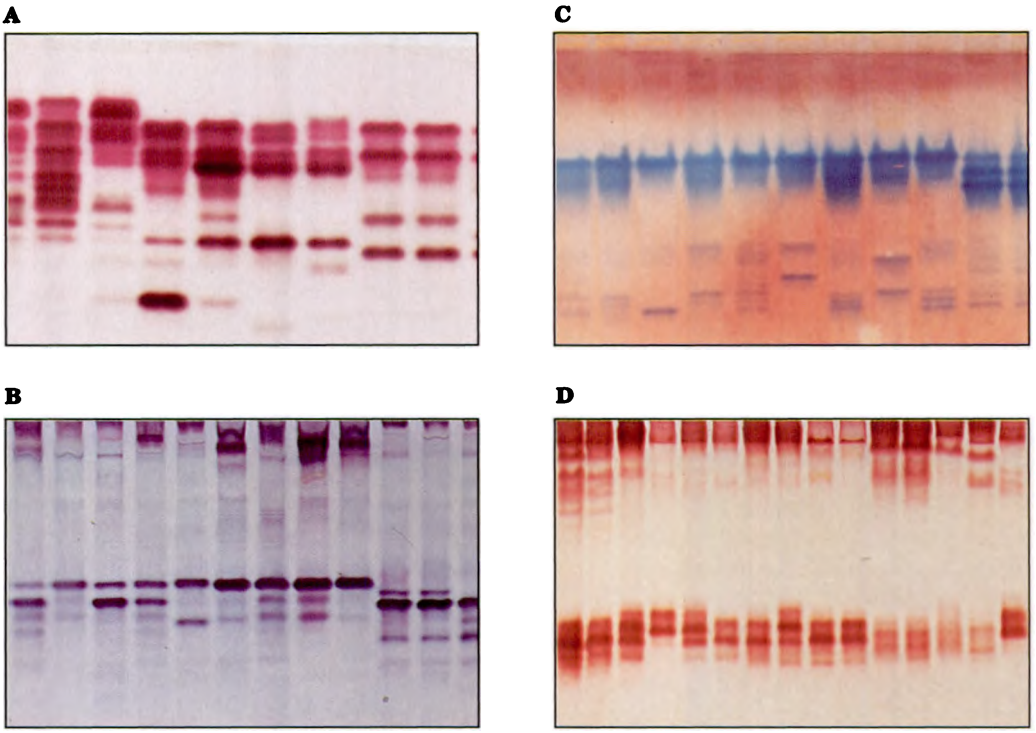

Figure 2. Zymograms of *Brachiaria* species and accessions of the polymorphic isozymes (A) αß-EST, (B) DIA, (C) GOT, and (D) PRX: from left, *B. brizantha* CIAT 6294, 6780, 6012, and 26646; *B. decumbens* CIAT 606, 26180, 16494, and 26306; *B. ruziziensis* CIAT 6291 and 26175; *B. humidicola* CIAT 679, 6013, and 6133; and *B. dictyoneura* CIAT 16508 and 16189 (C. M. Meghji, B. L. Maass, and C. H. Ocampo, unpublished data).

Table 7. Banding patterns resulting from electrophoretic analysis of glutamate oxaloacetate transaminase (GOT), peroxidase (PRX), and diaphorase (DIA) isozymes in 416 accessions of five species of *Brachiaria* germplasm.

Banding patterns	GOT	PRX	DIA	Across all three isozymes
B. brizantha, B. decumbens, B. ruziziensis (340 accessions)				
Unique banding patterns (no.)	53	17	13	242
Unique banding patterns (%)	16	5	4	71
Total of distinct patterns (no.)	103	45	22	277
Total of distinct patterns (%)	30	13	7	81
B. humidicola, B. dictyoneura (76 accessions)				
Unique banding patterns (no.)	18	3	8	42
Unique banding patterns (%)	24	4	11	55
Total of distinct patterns (no.)	33	6	19	55
Total of distinct patterns (%)	43	8	25	73
Across all five species (416 accessions)				
Unique banding patterns (no.)	57	17	18	279
Unique banding patterns (%)	14	4	4	67
Total of distinct patterns (no.)	124	45	35	332
Total of distinct patterns (%)	30	11	8	80

SOURCE: C. M. Meghji and B. L. Maass, unpublished data.

Molecular markers, recent in the studies of genetic diversity of *Brachiaria*, are being applied to the mapping of the apomixis gene (Tohme et al., Ch. 13, this volume).

Conclusions and Recommendations

Collecting efforts, especially during the last decade, led to the acquisition of a large and highly diverse collection of *Brachiaria* germplasm (about 1,000 accessions of 33 species). This collection provides a solid base for the development of new *Brachiaria* cultivars through selection or plant breeding. Comprehensive studies conducted at the major centers of conservation document the genetic diversity available with regard to morphology, isozymes, reproductive biology, molecular markers, and agronomic traits. The results of the different characterizations of the collection now must be integrated with information on the environmental origin of the accessions.

Additional collection is needed for species where holdings are inadequate, and from regions that have been insufficiently explored or are particularly threatened by genetic erosion, especially as *Brachiaria* is not an important commercial crop in Africa (Ndikumana and Leeuw, Ch. 16., this volume). Our ability to manipulate apomixis and generate novel genetic variation by hybridization diminishes, to some extent, the urgency of additional germplasm collection, but only for species for which breeding is currently being done (Miles and Valle, Ch. 11, this volume).

Collection methodology needs to be improved to avoid losing ex situ germplasm through lack of viability in the original seed samples. Most existing collections of *Brachiaria* germplasm are maintained in the field, because of poor seed production and seed quality. Research is needed on seed physiology, including seed production and handling prior to storage, to overcome this problem and facilitate maintenance and distribution of germplasm as seed. Development of an in vitro conservation method would be useful for conserving accessions with seed production problems, and particularly for sexual biotypes.

Proper documentation of the world's *Brachiaria* germplasm is a prerequisite for its effective use. Thus, the major germplasm banks urgently need to compile and cross-reference their *Brachiaria* data into a catalog like the one compiled for the tropical legume, *Centrosema* (Schultze-Kraft et al., 1989). So far, only parts of different *Brachiaria* collections have been duplicated at the major centers of conservation. For safety, effort should be made to duplicate all collections.

All *Brachiaria* species that have attained importance as forage plants occur naturally in eastern Africa, which represents a center of diversity of the genus. That region has numerous natural reserves that may offer an excellent opportunity for in situ conservation. For this purpose, inventories should be compiled of *Brachiaria* species in natural reserves, and studies conducted on their genetic diversity and stability in such areas.

Acknowledgments

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To save space, the following acronyms are used in place of publishers' names:

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

CSIRO = Commonwealth Scientific and Industrial Research Organisation

FAO = Food and Agriculture Organization of the United Nations

FEALQ = Fundação de Estudos Agrários "Luiz de Queiroz"

FONAIAP = Fondo Nacional de Investigaciones Agropecuarias

ICA = Instituto Colombiano Agropecuario

IDIAP = Instituto de Investigación Agropecuaria de Panamá

INIA = Instituto Nacional de Investigaciones Agrícolas

INIFAP = Instituto Nacional de Investigaciones Forestales y Agropecuarias

MAG = Ministerio de Agricultura y Ganadería

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Agricultural Science

NZSAP = New Zealand Society of Animal Production

SARH = Secretaría de Agricultura y Recursos Hidráulicos

TGSA = Tropical Grasslands Society of Australia

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Appendix. Maps Showing the Natural Distribution of Seven *Brachiaria* Species.

Map 1. Natural distribution of *Brachiaria brizantha*.

Map 2. Natural distribution of *Brachiaria decumbens*.

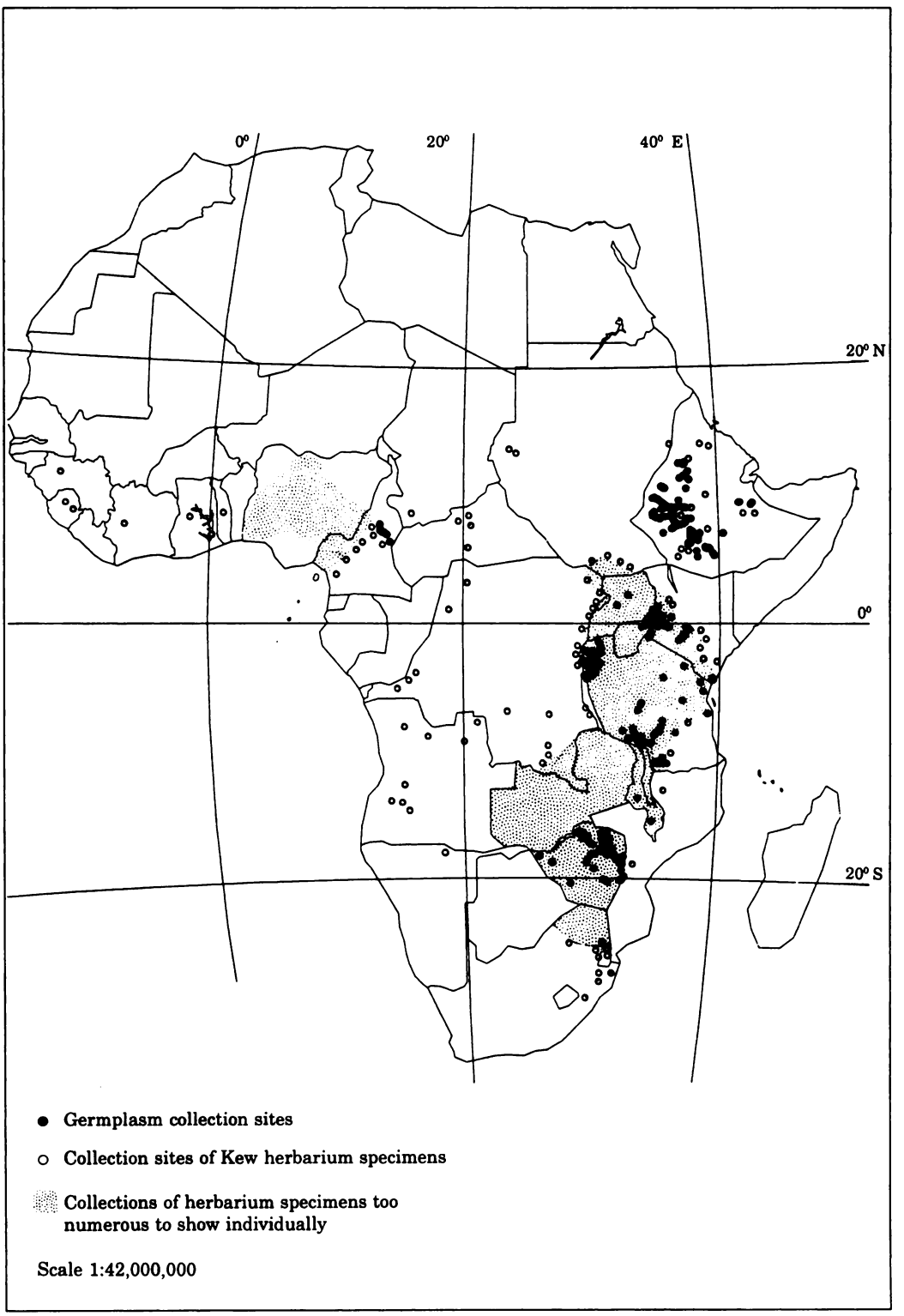
Map 3. Natural distribution of *Brachiaria ruziziensis*.

Map 4. Natural distribution of *Brachiaria humidicola*.

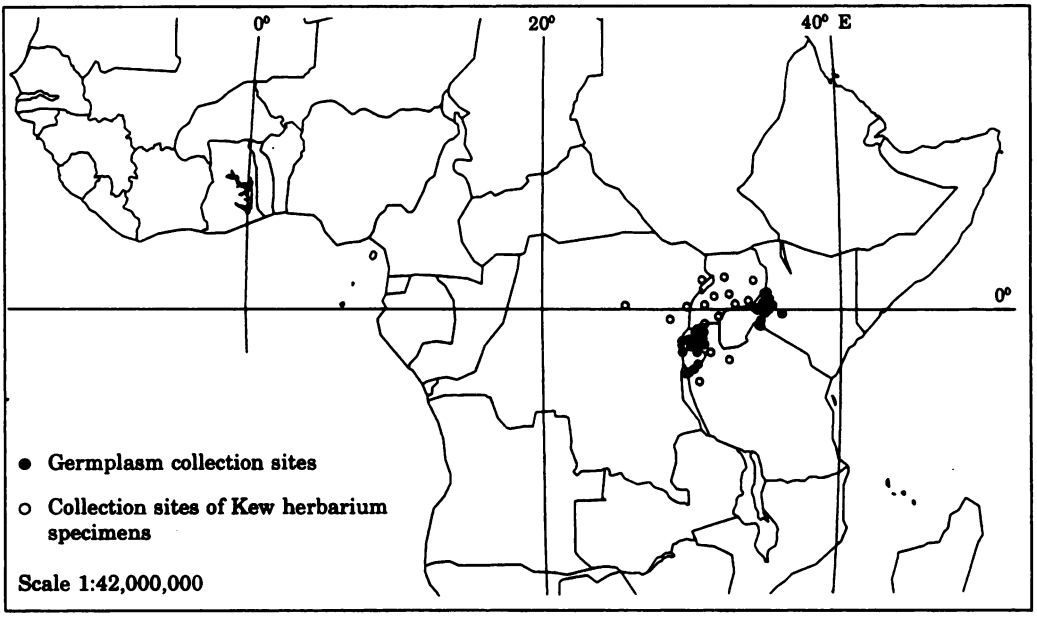
Map 5. Natural distribution of *Brachiaria dictyoneura*.

Map 6. Natural distribution of *Brachiaria jubata*.

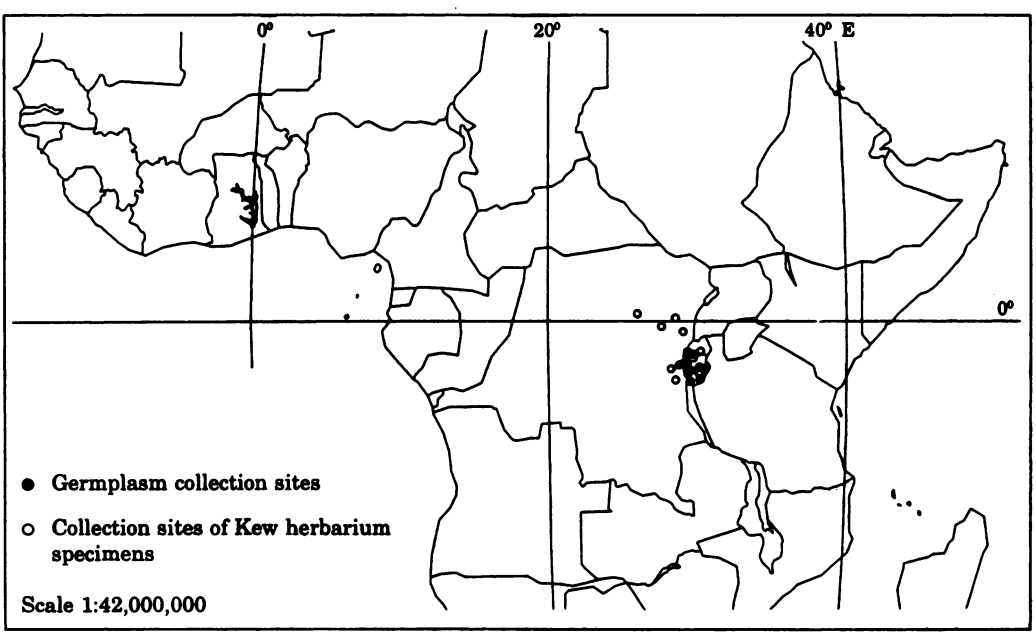
Map 7. Natural distribution of *Brachiaria nigropedata*.



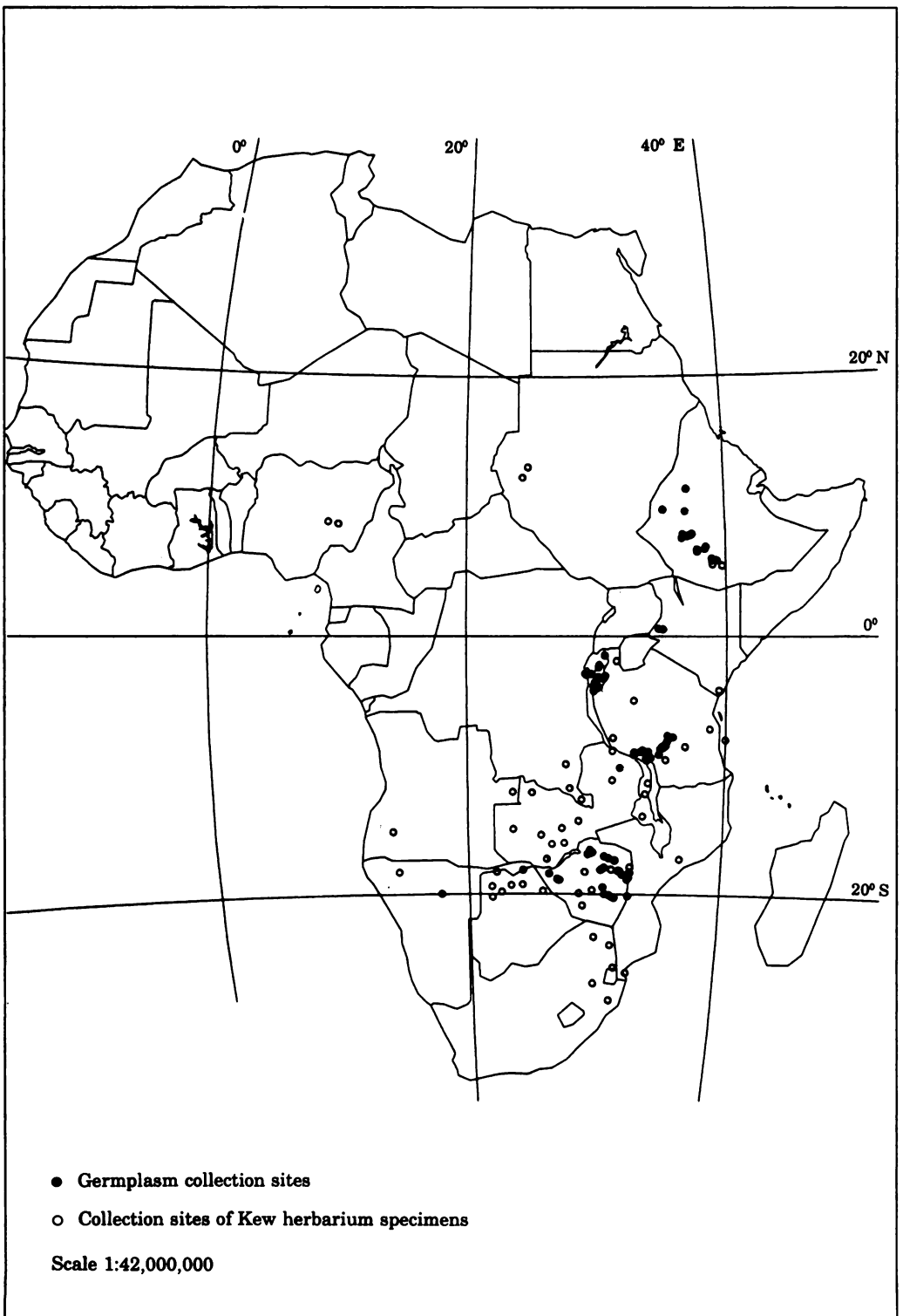
Map 1. Natural distribution of *Brachiaria brizantha*.



Map 2. Natural distribution of *Brachiaria decumbens*.



Map 3. Natural distribution of *Brachiaria ruziziensis*.



Map 4. Natural distribution of *Brachiaria humidicola*.

Chapter 3

The Agronomy and Physiology of *Brachiaria* Species

M. J. Fisher and P. C. Kerridge*

Abstract

This paper reviews published and unpublished information on the physiological and agronomic characteristics associated with the widespread adaptation of *Brachiaria* species. Adaptation to shade, drought, flooding, rainfall, and defoliation are discussed. Strong regrowth under frequent defoliation is a major factor in persistence; however, this attribute probably results in the adoption of grazing management practices that work against the persistence of most legumes sown in association with *Brachiaria*. The negative aspects of pasture degradation and the positive effects of carbon sequestration should stimulate a search among new *Brachiaria* accessions for the physiological and agronomic characteristics that will make the genus even more useful.

Introduction

The genus *Brachiaria* contains several commercial species, including *B. decumbens*, *B. dictyoneura*[1], *B. humidicola*, *B. brizantha*, and *B. ruziziensis*, each of which has been released in one or more tropical American countries (Miles and Lapointe, 1992; Keller-Grein et al., Ch. 2, this volume). These *Brachiaria* species are probably the most widely distributed sown forage grasses in the tropics; Brazil has at least 35 million hectares of sown pastures (Vera et al., 1992)—although current undocumented estimates put the figure at more than 70 million hectares. Between 1972 and 1975, Brazil imported more than 2,000 t of seed of *B. decumbens* cv. Basilisk from Australia (Thomas and Grof, 1986); Brazil now produces about 100,000 t of *Brachiaria* seed annually (Santos Filho, Ch. 9, this volume). However, despite the commercial importance of these species, previous reviews (Loch, 1977; Thomas and Grof, 1986) gave little information on the physiological and agronomic characteristics that contribute to this remarkable diffusion. Here, we examine the characteristics that contribute to the successful adaptation of *Brachiaria* grasses.

Physiology

Data on the physiology of *Brachiaria* species are limited; where available, they are often for relatively less important species than those in extensive commercial use.

The photosynthetic characteristics of leaves of *B. ruziziensis* in growth chambers were compared with nine other tropical grass species (Table 1). The rate of net leaf photosynthesis, the initial slope of its light response curve, and its light-use efficiency at maximum net photosynthesis were lower than those of the other grasses, probably because its leaf conductance was also the lowest of the group (Ludlow and Wilson, 1971). Dark respiration and light compensation were in the lower third of the 10 species. The temperature response of photosynthesis was similar in six of the species, including *B. ruziziensis*. Dark respiration increased logarithmically

* Tropical Lowlands Program and Tropical Forages Program, respectively, CIAT, Cali, Colombia.

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Table 1. Characteristics of leaf photosynthesis of *Brachiaria ruziziensis* compared with means of nine other tropical grass species.

Characteristic	*B. ruziziensis*	Mean of nine grasses[a]
Net photosynthesis (P_N)[b] (μmol $CO_2/m^2/s$)	29.0	31.6-46.1
Leaf conductance (C_l) (mmol/m^2/s)	123	150-290
Dark respiration (R_D) (μmol $CO_2/m^2/s$)	2.7	2.2-4.1
R_D/P_N (%)	9.0	4.0-13.0
Light compensation point (μE/m^2/s)	34.2	19.0-42.8
Initial slope of light response curve (mol CO_2/E)	0.083	0.083-0.120
Efficiency of maximum net photosynthesis (mol CO_2/E)	0.037	0.060-0.080

a. *Cenchrus ciliaris, Chloris gayana, Melinis minutiflora, Panicum coloratum, P. maximum* var. *trichoglume, P. maximum, Pennisetum purpureum, Setaria sphacelata, Sorghum almum.*

b. P_N (Net photosynthesis) and C_l (leaf conductance) were measured at 280 ± 5 μL/L CO_2 concentration and 1,900 μE/m^2/S radiation flux density.

SOURCE: Ludlow and Wilson, 1971.

between 10 and 50 °C, while only small differences were found among grasses in the minimum, optimum, and maximum temperatures for photosynthesis (means of 7.0, 38.3, and 57.3 °C, respectively).

Climatic Adaptation

In the Cauca Department of Colombia (3° N), a strong interaction has been observed between performance and altitude. Growth is slower at 1,600 m than at 1,200 m. In contrast, flowering, seed production, and seed quality are markedly greater at the higher altitude, especially in *B. humidicola* (B. L. Maass, 1994, personal communication), which normally does not produce seed at low latitudes. Presumably, this is because of the difference in temperature between the two sites. This apparent effect of temperature needs to be investigated further, as it has important implications for the release and adoption of new *Brachiaria* cultivars in tropical areas. Flowering and seed production are discussed further by Hopkinson et al. (Ch. 8, this volume).

Loch (1977) assessed *B. decumbens* as better adapted to the humid tropics in Australia, with a dry season of less than 4 months and an annual rainfall of more than 1,400 mm. In the American humid tropics, the use of *B. decumbens* is restricted not by physical, but by biotic constraints (Valério et al., Ch. 6, this volume). In the strongly seasonal climate of the isothermic savannas of the Brazilian Cerrados, however, *B. decumbens* cv. Basilisk is grown in areas where the dry season is as long as 7 months and rainfall as low as 1,300 mm. It extends further into drier zones than *B. humidicola*. *Brachiaria brizantha* is reputed to tolerate drought better (Thomas and Grof, 1986) than either *B. decumbens* or *B. humidicola*. All three species grow well throughout the year in the piedmont of the eastern cordillera of the Andes in Colombia, where rainfall is more than 4,000 mm.

Agronomic Characteristics

In an experiment at the CNPGC of EMBRAPA at Campo Grande in the Brazilian Cerrados, Valle et al. (1993) compared the agronomic characteristics of 184 accessions of *Brachiaria* (Table 2). On the basis of cluster analysis, they concluded that several *B. brizantha* accessions were the highest leaf producers, with better seasonal distribution of production, and fast, dense regrowth after defoliation. These findings complement those of Grof et al. (1989) in which 343 accessions of *Brachiaria*

Table 2. Agronomic characteristics of 13 accessions chosen from 184 accessions of *Brachiaria* in Campo Grande, MS, Brazil.

Species	Acc. (no.)	Annual yield of leaf dry matter (t/ha)	Dry-season leaf production (%)	Leaf:stem ratio in dry and wet seasons	Regrowth score[a]
B. brizantha	7	11.8-21.0	0.20-0.35	1.24-2.57	3-5
mean		16.3	0.27	1.66	3.6
cv. Marandu		10.8	0.26	2.64	4
B. decumbens	1	11.4	0.26	1.07	4
cv. Basilisk		10.2	0.31	1.51	3
B. humidicola	1	8.6	0.13	1.66	4
commercial		5.2	0.20	2.38	3
B. jubata	1	8.6	0.16	1.20	3

a. 0 = very poor, 6 = excellent.

SOURCE: Valle et al., 1993.

species were evaluated at Planaltina, Brazil, at the Centro de Pesquisa Agropecuária dos Cerrados (CPAC) of EMBRAPA. Cluster analysis grouped the most productive accessions (17-22 t/ha per year) into three clusters in which 82.5% of the accessions were *B. brizantha* with erect to semierect growth habit. These accessions were also strongly stoloniferous. This type of growth habit in *Brachiaria* is therefore probably strongly associated with good production and adaptation.

However, at Carimagua, in the Eastern Plains of Colombia, an accession of *B. brizantha* (CIAT 664, now reclassified as *B. decumbens*) was the least productive of five *Brachiaria* accessions grown with *Desmodium ovalifolium* under rotational grazing (Table 3). Of the three highest yielding accessions, *B. humidicola* CIAT 679 and *B. dictyoneura* CIAT 6133 were released as cultivars 'Humidícola' and 'Llanero', respectively (Miles and Lapointe, 1992). The marked difference in yields between 1983 and 1984 is the result of different management. The first-year data are for establishment yields of ungrazed plots, whereas the second-year data are for presentation yields under grazing. The accession CIAT 664 is not well adapted to the low-fertility soils of the area.

Table 3. Presentation yields of five *Brachiaria* species grown in association with *Desmodium ovalifolium* (mean of eight accessions) at Carimagua, Colombia.

Species (accession)	Annual DM yield[a] (t/ha)	
	1983	1984
B. brizantha (CIAT 664)[b]	7.3 c	1.3 c
B. decumbens (CIAT 665)	11.5 b	1.6 bc
B. dictyoneura (CIAT 6133)	11.7 b	2.0 b
B. humidicola (CIAT 679)	14.5 a	3.1 a
Brachiaria sp. (CIAT 6298)	7.7 c	1.6 bc

a. Yields followed by the same letter do not differ significantly ($P>0.05$).

b. Reclassified as *B. decumbens* (S. A. Renvoize, 1993, unpublished report).

SOURCES: CIAT [1984]; 1985.

Brachiaria species show rapid regrowth and good persistence under heavy or frequent defoliation (Rika et al., 1991). *Brachiaria decumbens* ranked higher over 10 harvests under cutting (Table 4), compared with the other species; under grazing, *B. decumbens* persisted longer than *Panicum maximum* and *Digitaria setivalva* (now *D. milanjiana*) under increasing stocking rates and heavy grazing pressure (Chen et al., 1981). As grazing pressure increased, the pasture of *P. maximum* was gradually invaded by *Paspalum conjugatum*, unlike that of *B. decumbens* pasture, which

Table 4. Growth rates (kg/ha per day)[a] of three *Brachiaria* accessions compared with those of 20 other grasses under coconuts in North Sulawesi, Indonesia.[b]

Species	Harvests (2-month intervals)			
	1-3	4-6	7-10	Mean of 10 harvests
B. decumbens cv. Basilisk	100.7 (4)	55.1 (1)	49.6 (1)	66.7 (1)
B. decumbens (local)	58.6 (16)	52.1 (2)	49.6 (1)	53.1 (6)
B. humidicola cv. Tully	83.8 (6)	49.1 (4)	35.2 (7)	56.9 (5)
Mean of 23 species[c]	74.8	37.1	29.1	45.2
Range	231.1-34.6	55.1-21.8	49.6-29.1	104.0-27.3

a. Numbers in parentheses: rank among 23 accessions.

b. Mean annual rainfall = 2,700 mm, evenly distributed, with a somewhat reduced incidence for 3 months; soil = fertile sandy loam, pH = 6; light transmission under coconuts = 73%.

c. Accessions ranking 24 onward in the original 36 were eliminated as poorly adapted.

SOURCE: Kaligis and Sumolang, 1991.

maintained high ground cover until it "crashed" under prolonged and heavy grazing at a stocking rate of 10 head/ha.

Shade tolerance

Brachiaria species are used as soil covers in many plantation crops, such as rubber and coconut, in Southeast Asia and the Pacific Islands (Stür et al., Ch. 17, this volume). Their tolerance of shade is therefore of interest. Thirty-five forage grass accessions were grown under coconut on fertile soils in North Sulawesi and Bali, Indonesia, with light transmissions of 73% or 58%, respectively. Rainfall (amount and distribution) was confounded with light transmission: higher total rainfall and more even distribution occurred at the site with greater light transmission. *Brachiaria decumbens* cv. Basilisk was the top performer at the site with the higher rainfall, less shade, and a 12-month growing season (Table 4) (Kaligis and Sumolang, 1991). It was also one of the better performers at the site with the lower rainfall, more shade, and a more marked dry season (Table 5) (Rika et al., 1991). *Brachiaria humidicola* performed relatively better at the site with higher rainfall and less shade (rank 5) than at the one with lower rainfall and more shade (rank 16).

Table 5. Growth rates (kg/ha per day)[a] of three *Brachiaria* accessions compared with those of 19 other grasses under coconuts in Bali, Indonesia.[b]

Species	Rainy season	Dry season	Annual mean
B. brizantha CPI 15890[c]	35.7 (10)	14.8 (19)	30.0 (10)
B. decumbens cv. Basilisk	36.0 (9)	24.8 (5)	33.0 (9)
B. humidicola cv. Tully	24.5 (18)	18.4 (12)	22.9 (16)
Mean of 22 species[d]	33.9	19.6	30.0
Range	54.4-20.6	31.3-12.0	47.4-18.8

a. Numbers in parentheses: rank among 22 accessions.

b. Mean annual rainfall = 2,070 mm, with a 7-month rainy season and a distinct 3-month dry season; soil = fertile sandy clay loam, pH 6-7; light transmission under coconuts = 58%.

c. = CIAT 6674 (syn. CIAT 26567); BRA-000329.

d. Accessions ranking 23 onward in the original 35 were eliminated as poorly adapted.

SOURCE: Rika et al., 1991.

Shelton and his colleagues (1987) classified some *Brachiaria* species in commercial use according to published data on their ability to tolerate shade. *Brachiaria miliiformis* (now *B. subquadripara*) was highly shade tolerant; *B. brizantha*, *B. decumbens*, and *B. humidicola* were all intermediate; and *B. mutica* had low tolerance.

Drought tolerance

At two sites, with contrasting soils, on the Caribbean island of Martinique, Gayalin (1994) compared the performance of *B. decumbens* with *Panicum maximum*, *Pennisetum purpureum*, and *Tripsacum laxum* as forages for deferred grazing in the dry season. Although *B. decumbens* is widely grown by farmers for its drought resistance, it was outyielded by *T. laxum*, which retained three to seven times more green leaf; *P. purpureum* yielded two to three times more total forage than *B. decumbens* and had between one and three times as much green leaf dry matter (DM) (Table 6). Obviously, farmers' perception of drought resistance, probably on the basis of the apparent proportion of green leaf in the standing forage, was not a good guide to the amount of green leaf actually present in the forage.

Compatibility with legumes

Thomas and Grof (1986) and Loch (1977) noted that, because *Brachiaria* species are very aggressive, they had been difficult to grow in long-term, stable associations with legumes. *Desmodium heterophyllum* and *D. ovalifolium* were reported to be more compatible with *Brachiaria* than species of *Centrosema* and *Pueraria*, which, in turn, were more compatible than *Stylosanthes guianensis*. Of the common cultivars of *Brachiaria*, *B. humidicola* is regarded as being the most aggressive, followed by *B. dictyoneura* CIAT 6133, then *B. decumbens*. There are no data, nor even an objective measure, for this ranking. Usually, few weeds invade a *Brachiaria* pasture unless it is grossly mismanaged through overgrazing.

Some legumes, grown in association with *B. decumbens*, have persisted over the long term, for example, at Carimagua, associations of *B. decumbens-Stylosanthes capitata* on a sandy soil (M. J. Fisher, unpublished data). *Brachiaria decumbens-Pueraria phaseoloides* persisted for more than 10 years on a clay loam (Lascano and Estrada, 1989; Lascano and Euclides, Ch.7, this volume), even though, in some years, the vigor of *B. decumbens* was reduced by spittlebug infestation. At Pucallpa, Peru, associations of *B. decumbens-D. ovalifolium* have persisted for 8 years under lenient grazing (R. R. Vera, 1994, personal communication).

Fisher and Thomas (1989) measured regrowth in grass-legume pastures based

Table 6. Forage for deferred grazing at the end of the dry season, using four grasses in two pedoclimatic zones of Martinique.

Species	Southern dry zone[a]			Northwestern dry zone[b]		
	DM yield (t/ha)	Proportion of green leaf (%)	Green leaf yield (t/ha)	DM yield (t/ha)	Proportion of green leaf (%)	Green leaf yield (t/ha)
Brachiara decumbens	10.5	12	1.3	11.7	12	1.4
Panicum maximum	-	-	-	9.7	18	1.7
Pennisetum purpureum	22.3	15	3.3	32.2	7	2.3
Tripsacum laxum	22.4	41	9.2	14.3	34	4.9

a. Rainfall = 1,400 mm; soil = Vertisol.

b. Rainfall = 1,500 mm; soil = volcanic sand.

SOURCE: Gayalin, 1994.

on *Brachiaria* species, which were grazed rotationally at two levels of forage allowance for 2 years. A good relationship was found between residual leaf area at the start of the regrowth phase and the growth rate of each component of the pastures. Thus, *Brachiaria*-based pastures can be managed so to maintain legumes. In some cases, growth rate was lower than expected, probably a result of excess soil water during wet months.

The legume *Arachis pintoi* is now well known to be especially compatible with *Brachiaria* species (Fisher and Cruz, 1994). In the Colombian Llanos, it persisted for 4 years in *B. humidicola* pastures at stocking rates of 2-4 head/ha (Lascano, 1994). At the higher stocking rate and during the dry season, DM yields were very low, but weed invasion was negligible, even after 5 years.

In an experiment at Carimagua, pastures with different proportions of *A. pintoi* and *B. dictyoneura* cv. Llanero were each grazed at three levels of forage allowance for 3 years. The proportion of legume increased, irrespective of forage allowance or starting composition (Fisher and Cruz, 1994). This indicates a considerable ability of the legume to form stable associations with the grass, although the precise mechanisms are not clear.

Research in Costa Rica (Ibrahim et al., 1994) confirms that *A. pintoi* is more persistent than other legumes in associations with *Brachiaria*. The proportion of *A. pintoi* increased with heavy grazing pressure, and fewer weeds grew in these than in the other *Brachiaria*-legume associations (Table 7). One mechanism for greater persistence was the greater half-life of *A. pintoi* plants. A striking feature of this work was the poor performance of *B. humidicola*.

Ayarza et al. (1994) measured root and shoot biomass in pure stands of *A. pintoi* or *B. decumbens* and in an association of the two species under grazing (Table 8). They concluded that, because of competition from the grass, the legume in the association had a lower root biomass than the legume alone. But shoot biomass was much higher in the association than in either pure sward, because the presence of the legume stimulated the grass, presumably by contributing N.

In summary, it is difficult to assess whether the poor persistence of legumes (other than *A. pintoi*) with *Brachiaria*

Table 7. Percentage of dry weight[a] of legume, grass, and volunteer species in a grazing experiment, Guápiles, Costa Rica.

Species[b] (accession no.)	Stocking rate (head/ha) on:			
	B. brizantha (CIAT 6780)		*B. humidicola* (CIAT 6369)	
	1.75	3.0	1.75	3.0
Arachis pintoi (CIAT 17434)	8.4	17.8	23.3	44.1
Grass	89.5	77.5	72.9	49.7
Volunteer species	2.1	4.7	3.8	6.2
Stylosanthes guianensis (CIAT 184)	1.2	1.4	14.5	6.3
Grass	96.0	89.4	75.7	82.5
Volunteer species	2.8	9.0	9.8	11.2
Centrosema macrocarpum (CIAT 5713)	1.0	1.8	2.5	4.5
Grass	90.0	93.4	8.7	36.1
Volunteer species	9.0	4.8	88.8	59.4

a. Over the last 5 of 17 grazing cycles.

b. The proportion of grass was calculated by difference.

SOURCE: Ibrahim et al., 1994.

Table 8. Standing root (0-100 cm) and shoot biomass, and root-to-shoot ratios in pastures of *B. decumbens* (CIAT 606) and *Arachis pintoi* (CIAT 17434), alone or in association, Carimagua, Colombia.

Pasture	Root biomass (kg/ha)	Shoot biomass (kg/ha)	Total (kg/ha)	Root-to-shoot ratio
B. decumbens alone	2647 ± 620	2184 ± 320	4831	1.21
A. pintoi alone	3404 ± 352	2240 ± 603	5844	1.52
Grass-legume association	2674 ± 420	4512 ± 118	7186	0.60

SOURCE: Ayarza et al., 1994.

species results from competition with the grass or from inherent characteristics of the legumes. Most other legumes have characteristics that do not favor persistence under heavy defoliation; that is, easily removed growing points and low seed production. *Brachiaria decumbens* tolerates heavier grazing than other grasses (Chen et al., 1981) and thus tends to be grazed more heavily; this in turn puts greater pressure on the legumes. On the contrary, where growing points are not removed, as with *A. pintoi*, the proportion of legume can increase under heavy defoliation (Ibrahim et al., 1994).

Response to flooding

We could find no data in the literature comparing species, accessions, or cultivars of *Brachiaria* for tolerance of flooding, although observations in the poorly drained savannas of southwestern Venezuela, where *Brachiaria* species are widely sown, suggest that flooding has a profound and differential effect on species survival (M. J. Fisher, personal communication). In relatively well-drained areas, *B. decumbens* dominates; in intermittently flooded areas, *B. humidicola* dominates; and a clear line separates the two. Where water stands for more than a few weeks, neither survives. However, *B. arrecta* (syn. *B. radicans*) appears able to tolerate prolonged flooding, and *B. mutica* can grow well in shallow water for long periods. Argel and Keller-Grein (Ch. 14, this volume) report preliminary data showing *B. humidicola* as performing better than *B. brizantha* accessions under waterlogged conditions in Costa Rica. We can only speculate on the mechanisms, but they could be associated with differential ability to take up N in the nitrate or ammonium form (I. M. Rao, 1994, personal communication). No anatomical studies have been undertaken to determine if *B. arrecta* has aerenchyma-like structures that permit it survive prolonged flooding.

Carbon Sequestration

Fisher et al. (1994) have recently shown that both *B. humidicola* and *Andropogon gayanus* sequester C deep in the soil in the Colombian Eastern Plains. When grown with the legume *A. pintoi*, *B. humidicola* fixed 70.4 t of C to 80 cm in the soil in 9 years, while the grass alone fixed 25.9 t (Table 9). The absolute amounts were undoubtedly underestimated by limiting sampling to 80 cm. The contribution of the legume, which was introduced in 1987, may be estimated, by the difference, at 44.5 t/ha (5 t/ha per year), although the contribution of the legume to root biomass was only about 20%. Given the large areas sown to *Brachiaria* species in Brazil, if all the *Brachiaria* species behave similarly, the amount of C being sequestered could be of global importance in mitigating the greenhouse effect.

Degradation of *Brachiaria* Pastures

Farm pastures of *Brachiaria* species often degrade with time, declining in productivity with an ingress of weeds. However, the processes of degradation are poorly described and understood. For example, two old pastures of pure grass at Carimagua, one of *B. decumbens* and the

Table 9. Soil carbon in native savanna and sown pastures based on *Brachiaria humidicola*, Carimagua, Colombia.

Depth (cm)	Savanna, C in layer (t/ha)	Sown pasture			
		B. humidicola alone		*B. humidicola-Arachis pintoi*	
		C in layer (t/ha)	Difference from savanna (t/ha)[a]	C in layer (t/ha)	Difference from savanna (t/ha)
0-20	70.3	76.0	5.7 ± 4.3 NS	88.1	17.8 ± 4.2 **
20-40	52.4	57.6	5.3 ± 3.2 NS	71.2	18.6 ± 6.0 **
40-80	74.3	89.2	14.9 ± 6.2 *	108.4	34.0 ± 10.0 **
Total	197.1	222.8	25.7 ± 7.7 **	267.5	70.4 ± 15.5 ***
Percentage of increase below 20 cm	-	-	78.0	-	74.7

a. Differences quoted are ± SE, where SE is the standard error of difference between the means (n = 12).
NS = $P>0.05$, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

SOURCE: Fisher et al., 1994.

other of *B. humidicola*, show little degradation (Lascano and Euclides, Ch. 7, this volume). The first, now 16 years old, has received modest amounts of nonnitrogenous maintenance fertilizer every second year and is grazed more leniently than most farm pastures, but, despite repeated attacks of spittlebug, it has not degraded. The second has received no maintenance fertilizer and is managed more like farm pastures, yet this pasture shows no evidence of degradation either. We have no explanation, but clearly there is much to be understood in the process of degradation and its causal factors. Boddey et al. (Ch. 5, this volume) suggest that nitrogen fixation by bacteria associated with the grass may be involved.

Conclusions

Brachiaria species readily adapt to low-fertility soils of the South American savannas largely because they tolerate soil conditions of high Al and low P and Ca (Rao et al., Ch. 4, this volume). They can also withstand heavy and frequent defoliation and resist weed ingress. This adaptability does not appear to come from physiological characteristics such as light-use efficiency, shade tolerance, flooding tolerance, and/or other factors associated with climatic adaptation. Because of the range of species, the genus as a whole shows such wide adaptation that intensive physiological studies have, so far, not been needed. Nevertheless, some instances of poor adaptation, plus the complexity of factors associated with general pasture degradation, point to the need for more ecophysiological research.

Future Research Needs

We pose future research needs as a series of questions, arranged in a logical sequence by category. We do not attempt to prioritize them.

Grass-legume associations

Why has *B. humidicola* in association with *A. pintoi* failed at Guápiles, Costa Rica, but persisted (and continues to persist) at Carimagua at the same stocking rates?

What are the attributes required in grasses to be grown in association with a legume as opposed to pure grass pastures?

In the context of grass-legume associations, is reduced vigor of *B. decumbens* cv. Basilisk from spittlebug

susceptibility necessarily bad? Conversely, what is the role of spittlebug damage in maintaining the legume component balance?

Do we really need more vigorous grasses? Should we not focus more on total digestible nutrients, shown to be negatively correlated with DM yield? G. W. Burton at Georgia was outstandingly successful in using digestibility as a breeding criterion in *Cynodon dactylon* (Burton, 1972; Chapman et al., 1972).

Pure grass pastures

What are the factors that cause pasture degradation?

Can degradation be prevented in pure grass swards?

Why have the pure grass pastures of *B. decumbens* or *B. humidicola* on heavy soils at Carimagua not degraded? Is this a special situation because of soil/drainage, management (including fertilizer), both, or none of these?

Carbon

What is the pathway of C storage in soil? Does it reflect plant net primary productivity, or are the roots important in themselves?

Is it feasible to select plants that partition more resources to roots? If so, what is the cost in terms of forage yield and animal performance? Can extra partitioning of C to roots be compensated by greater partitioning of C to leaves than stems in the shoot?

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To save space, the following acronyms are used in place of publishers' names:

ACIAR = Australian Centre for International Agricultural Research

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

INRA = Institut national de la recherche agronomique

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Agricultural Science

NZSAP = New Zealand Society of Animal Production

TGSA = Tropical Grasslands Society of Australia

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Chapter 4

Nutritional Requirements of *Brachiaria* and Adaptation to Acid Soils

I. M. Rao,* P. C. Kerridge,* and M. C. M. Macedo**

Abstract

Most commercial *Brachiaria* species are adapted to low-fertility acid soils of the tropics. We describe, with examples, some of the attributes that enable them to adapt. These include the ability to (1) maintain root growth at the expense of shoot growth; (2) acquire and use both nitrate and ammonium forms of N; (3) acquire N through associative fixation; (4) acquire P through extensive root systems and association with vesicular-arbuscular mycorrhizae; and (5) acquire Ca through extensively branched roots with large numbers of root tips. Although *Brachiaria* species have much lower internal requirements, especially of P and Ca, than do other grasses such as *Panicum maximum*, they show interspecific differences, which we describe. We also developed a system to diagnose mineral nutrient disorders by visual symptoms in *B. decumbens* cv. Basilisk, and describe our results. We offer a list of priorities for further research.

Introduction

The genus *Brachiaria* is pantropical, with its center of diversity in Africa (Parsons, 1972). Several species are now widely used in lowland agroecosystems (savannas and cleared forest regions) of the humid and subhumid tropics, particularly in South America, providing important sources of feed for ruminant livestock (Thomas and Grof, 1986). Of the perennial species, *B. decumbens*, *B. humidicola*, *B. brizantha*, and *B. dictyoneura*[1] have attained major economic importance.

Foliar anatomy of *Brachiaria* indicates the presence of two complete sheaths, with centrifugal chloroplasts in the outer sheath (Thompson and Estes, 1986). Most of the species use the PEP-CK (phosphoenolpyruvate carboxykinase) type of C_4 photosynthetic pathway (Gutiérrez et al., 1976; Oliveira et al., 1973).

Knowing how *Brachiaria* species adapt to low-fertility acid soils and what their nutritional requirements are is important, because nutrients are almost never present in optimal amounts for forage production. Consequently, plants are always compensating for stresses imposed by their nutritional environment. The relative importance of different soil nutrients in growth and productivity depends on the physiological adaptation of the species. Moreover, adaptation to acid soils strongly influences and is influenced by other biotic and abiotic stresses.

In acid soils, some mineral elements (e.g., P) may be deficient, whereas others (e.g., Al) are potentially toxic (Foy, 1988; Marschner, 1991). Variation in the mineral profiles among genera, species, and ecotypes of tropical grasses grown on the same soil and cut at a similar stage of maturity reflects the differences in acquisition and use of nutrients for plant growth. Clearly, farmers need grasses capable of extracting and supplying the required amounts of nutrients for the grazing ruminant.

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1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Paulino et al. (1987) and Malavolta and Paulino (1991) reviewed the literature on the main aspects of mineral nutrition of *Brachiaria* species. They compiled information on responses to macro- and micronutrients, and on mineral nutrient composition of the forage and its relationship to animal nutrition.

In this chapter we review the available information on the edaphic adaptation and response to fertilizer of *Brachiaria* species as a basis for suggesting future research priorities. Most information has been generated on very few genotypes, and the variation within species is almost unknown.

Adaptation to Acid Soils

The main constraints of acid soils are Al and/or Mn toxicities, and deficiencies of essential nutrients, such as N, P, Ca, and Mg; these constraints must be alleviated for successful pasture establishment. Scientists must therefore identify ecotypes of *Brachiaria* species that are adapted to these infertile soils and can make the most efficient use of applied nutrients. Although many such ecotypes have already been identified empirically, little is known about the mechanisms of adaptation (Lapointe and Miles, 1992; Miles and Lapointe, 1992; Valle, 1991). Adapted genotypes have attributes that are linked to strategies for acquiring the essential nutrients in a low-pH, high-Al environment. Understanding these strategies is fundamental to developing more efficient and reliable techniques for screening large numbers of genotypes for tolerance of acid soils.

Brachiaria species adapt to a wide range of soil types, from Oxisols and Ultisols (low-fertility acid soils) to Alfisols and Mollisols (high-fertility neutral soils). They perform much better on acid soils than other grasses, such as *Panicum* species (Botrel et al., 1990a; Grof, 1985; Malavolta and Paulino, 1991; Miles and Lapointe, 1992; Paulino et al., 1987; Rao et al., 1993b; Spain, 1979; Thomas and Grof, 1986). They also perform well on moderately fertile to very fertile soils (Malavolta and Paulino, 1991; Paulino et al., 1987; Salinas and Saif, 1990; Thomas and Grof, 1986). However, in the tropics, their climatic adaptation is restricted by low temperatures at altitudes over 2,000 m above sea level (m.a.s.l.) or dry seasons of more than 6 months (Bogdan, 1977; Thomas and Grof, 1986). Some species of *Brachiaria* are better adapted to drought (*B. decumbens* and *B. brizantha*); others to poorly drained soils (*B. humidicola*, *B. mutica*, *B. arrecta*, and *B. plantaginea*). The major positive and negative attributes of different *Brachiaria* species are described in Table 1 and by Keller-Grein et al. (Ch. 2, this volume).

A greenhouse study comparing the widely used genotypes *B. dictyoneura* cv. Llanero, *B. decumbens* cv. Basilisk, *B. humidicola* cv. Humidícola, and *B. brizantha* cv. Marandu indicates that several shoot and root attributes may contribute to adaptation to low-fertility acid soils (Rao et al., 1992; Rao et al., 1993b). The four cultivars were grown on a sandy loam and on a clay loam from Carimagua, at low or high rates of fertilizer (CIAT, 1990; I. M. Rao, unpublished data). Shoot production was lower under low than under high fertility and was associated with a decline in leaf area production and an increase in leaf-to-stem ratio (Table 2). Specific leaf area, which is a measure of leaf expansion per unit dry weight, was lower for cv. Humidícola and cv. Llanero than for cv. Basilisk and cv. Marandu. Shoot growth was markedly less on the sandy loam than on the clay loam, presumably because of a lower organic matter content and therefore a lower supply of N.

Root growth was less affected by low fertility than shoot growth, indicating that an attribute of adaptation was a change in carbon partitioning. The root-to-shoot ratio of all species was higher on the sandy loam than on the clay loam. Root-to-shoot ratios of cv. Llanero and cv. Humidícola were significantly higher than those of cv. Marandu and cv. Basilisk.

Table 1. Major plant attributes of important *Brachiaria* species.

Species	Positive attributes	Negative attributes
B. decumbens	High productivity under intensive use, tolerance of low fertility, good performance under shade, good quality forage	Susceptibility to spittlebug, low adaptation to poorly drained soils, toxin (sporidesmin) production, susceptibility to foliar blight
B. brizantha	High productivity, spittlebug tolerance, responsiveness to fertilizer application, drought resistance, ability to spread and suppress weeds, ability to grow in shade, good quality forage	Low adaptation to poorly drained soils, need for moderately fertile soils, susceptibility to foliar blight
B. humidicola	Strongly stoloniferous habit with ability to root at stolon nodes, adaptation to low-fertility soils, ability to cover ground rapidly and compete with weeds, adaptation to poorly drained soils, low P and Ca requirements, some spittlebug tolerance	Low seed production at low latitudes, low dry matter digestibility, low N and Ca concentration in forage, susceptibility to rust infection
B. ruziziensis	Fast growth early in wet season, compatibility with legumes, high seed production potential, ease of establishment, good quality forage	Need for well-drained fertile soils, susceptibility to spittlebug and foliar blight, low competitiveness with weeds
B. mutica	Good adaptation to poorly drained soils	Poor quality forage when mature, poor performance in association with legumes
B. arrecta	Adaptation to poorly drained soils	Poor adaptation to low-fertility soils, susceptibility to spittlebug, high levels of nitrates in forage (toxic?)

SOURCES: Bogdan, 1977; Skerman and Riveros, 1990; CIAT, unpublished data.

Measurements of shoot nutrient uptake for cv. Marandu and cv. Basilisk showed that they acquired larger amounts of Ca from both soils at both fertilizer rates than cv. Llanero and cv. Humidícola; cv. Basilisk also acquired more N and P than the other three species (Table 3). Nitrogen-use and P-use efficiency (measured as g of shoot biomass produced per g of total nutrient uptake) was higher in cv. Basilisk and cv. Marandu than in the other two cultivars; Ca-use efficiency was higher in cv. Humidícola and cv. Llanero.

Adaptation to low nitrogen supply

The productive life of monospecific swards of *Brachiaria* species is limited by N supply. Alvim et al. (1990) compared the forage production of five *Brachiaria* accessions at three rates of applied N (0, 75, 150 kg/ha per year) on an Oxisol with 1.86% organic matter in an experiment conducted at the Centro Nacional de Pesquisa de Gado de Leite (CNPGL) of EMBRAPA, Coronel Pacheco, MG, Brazil. With no additional N supply, a *B. brizantha* accession gave the lowest and two accessions of *B. decumbens* the highest annual dry matter (DM) yields. However, *B. brizantha* was most responsive to N application (Table 4). The species least responsive to applied N were *B. ruziziensis* and *B. humidicola*.

On the same experimental plots, Botrel et al. (1990b) evaluated the influence of N supply on forage crude protein (CP) content and mineral nutrient composition. They found that in all five accessions, CP level increased with increasing rates of N. *Brachiaria*

Table 2. Influence of soil type and fertilizer application on plant growth characteristics of different *Brachiaria* cultivars.

Plant characteristic	Soil type[a]	Soil fertility[b]	Cultivars				LSD ($P = 0.05$)
			B. brizantha cv. Marandu	*B. decumbens* cv. Basilisk	*B. dictyoneura* cv. Llanero	*B. humidicola* cv. Humidícola	
Shoot biomass (g/pot)	Sandy loam	Low	4.3	5.9	4.3	4.3	
		High	19.0	22.0	18.7	14.1	
	Clay loam	Low	7.8	10.0	8.4	7.4	
		High	19.5	24.3	18.2	18.9	1.6
Root biomass (g/pot)	Sandy loam	Low	7.0	5.9	12.2	8.9	
		High	19.4	16.0	18.7	17.7	
	Clay loam	Low	8.7	6.6	11.1	8.9	
		High	16.2	10.6	16.0	14.1	3.5
Leaf area (cm^2/pot)	Sandy loam	Low	397	365	297	332	
		High	1,213	1,081	794	930	
	Clay loam	Low	628	652	635	501	
		High	1,507	1,500	1,034	795	219
Specific leaf area (m^2/kg)	Sandy loam	Low	14.9	14.5	10.5	11.7	
		High	14.2	18.4	11.1	12.3	
	Clay loam	Low	14.2	15.0	12.7	10.1	
		High	16.0	17.6	13.9	8.8	3.7
Leaf-to-stem ratio (g:g)	Sandy loam	Low	1.62	0.74	1.84	1.98	
		High	0.76	0.37	0.65	1.18	
	Clay loam	Low	1.31	0.77	1.49	2.01	
		High	0.95	0.54	0.65	0.90	0.26

a. Sandy loam = Oxisol with 17% clay; pH 5.1; 0.52% total C; exchangeable cations (cmol/kg) 0.7 Al, 0.13 Ca, 0.08 Mg, 0.03 K, 2.0 mg/kg extractable P (Bray II); 77% Al saturation.
Clay loam = Oxisol with 37% clay; pH 5.0, 2.0% total C; exchangeable cations (cmol/kg) 2.6 Al, 0.21 Ca, 0.1 Mg, 0.17 K, 2.1 mg/kg extractable P (Bray II); 89% Al saturation.

b. Low fertilizer level (kg/ha) = P 20, K 20, Ca 47, Mg 14, S 10.
High fertilizer level (kg/ha) = N 40, P 50, K 100, Ca 101, Mg 28, S 20, Zn 2, Cu 2, B 0.1, Mo 0.1.

SOURCE: I. M. Rao, unpublished data.

humidicola forage contained the least CP at all rates of N (Table 4).

At Itaguaí, RJ, Brazil, several accessions of *Brachiaria* species grown on a low-fertility acid Planosol gave good DM yields without added N fertilizer (Souto, 1977a; 1978). In general, *Brachiaria* species, especially the *B. decumbens* accession FL 902-4, were less responsive to N fertilizer than *Digitaria decumbens* (now *D. eriantha*) (Souto, 1977b).

Differential uptake and use of nitrogen forms. Forage species differ in uptake and use of different forms of N. Sylvester-Bradley et al. (1988) suggested that certain *Brachiaria* species (e.g., *B. humidicola*) may inhibit soil nitrification. The uptake and use of N-NO_3^- (nitrate) and N-NH_4^+ (ammonium) by three *Brachiaria* accessions were evaluated, using nutrient solution culture (CIAT, [1984]; J. G. Salinas, unpublished data). Measurements of DM production, N content in plant tissue, and final concentration of N-NO_3^- and N-NH_4^+ in the nutrient solution after 90 days of plant growth indicated that all three accessions (*B. decumbens* cv. Basilisk, *B. dictyoneura* cv. Llanero, and *B. humidicola* cv. Humidícola) performed better when the N was supplied as N-NO_3^-. When the N was supplied as N-NH_4^+, the growth of cv.

Table 3. Influence of soil type and fertilizer application on shoot nutrient uptake and nutrient-use efficiency of different *Brachiaria* cultivars.

Nutrient uptake and use	Soil type[a]	Soil fertility[b]	Cultivars				LSD ($P = 0.05$)
			B. brizantha cv. Marandu	*B. decumbens* cv. Basilisk	*B. dictyoneura* cv. Llanero	*B. humidicola* cv. Humidícola	
Shoot N uptake (mg/pot)	Sandy loam	Low	18	21	19	20	
		High	64	89	63	63	
	Clay loam	Low	39	52	46	50	
		High	90	116	94	117	16
Shoot P uptake (mg/pot)	Sandy loam	Low	3.0	3.7	2.8	3.3	
		High	14.0	14.0	11.5	10.1	
	Clay loam	Low	6.0	7.1	6.2	5.8	
		High	12.3	15.7	11.3	11.9	1.3
Shoot Ca uptake (mg/pot)	Sandy loam	Low	20	20	11	9	
		High	76	78	36	32	
	Clay loam	Low	26	28	17	15	
		High	59	65	30	31	11
N-use efficiency (g/g)[c]	Sandy loam	Low	130	152	79	86	
		High	175	195	145	118	
	Clay loam	Low	137	134	101	91	
		High	140	162	123	111	28
P-use efficiency (g/g)	Sandy loam	Low	779	948	502	422	
		High	935	1,067	888	722	
	Clay loam	Low	826	952	746	745	
		High	1,103	1,229	1,038	1,087	215
Ca-use efficiency (g/g)	Sandy loam	Low	217	294	381	451	
		High	263	297	525	435	
	Clay loam	Low	304	357	493	498	
		High	333	373	610	602	44

a. Sandy loam = Oxisol with 17% clay; pH 5.1; 0.52% total C; exchangeable cations (cmol/kg) 0.7 Al, 0.13 Ca, 0.08 Mg, 0.03 K, 2.0 mg/kg extractable P (Bray II); 77% Al saturation.
Clay loam = Oxisol with 37% clay; pH 5.0, 2.0% total C; exchangeable cations (cmol/kg) 2.6 Al, 0.21 Ca, 0.1 Mg, 0.17 K, 2.1 mg/kg extractable P (Bray II); 89% Al saturation.

b. Low fertilizer level (kg/ha) = P 20, K 20, Ca 47, Mg 14, S 10.
High fertilizer level (kg/ha) = N 40, P 50, K 100, Ca 101, Mg 28, S 20, Zn 2, Cu 2, B 0.1, Mo 0.1.

c. Grams of forage produced per gram of total nutrient uptake.

SOURCE: I. M. Rao, unpublished data.

Basilisk and cv. Llanero was inhibited at higher levels, whereas that of cv. Humidícola increased. These results indicate that cv. Humidícola absorbs and uses both forms of N.

Further studies were made of *B. humidicola* cv. Humidícola and *B. brizantha* cv. Marandu grown in nutrient solution to determine differences in $N\text{-}NO_3^-$ and $N\text{-}NH_4^+$ uptake patterns under conditions that simulate grazing (Castilla and Jackson, 1991). These studies confirmed that cv. Marandu can take up only small quantities of $N\text{-}NH_4^+$ from nutrient solution, but cv. Humidícola can take up both forms of N. The authors suggested that this capacity may be part of the mechanism of adaptation of cv. Humidícola to acid soils; this attribute may also be one reason why cv. Humidícola is better adapted to wet environments than cv. Marandu.

Table 4. Effect of N application rate on annual dry matter production and crude protein concentration in forage of different accessions of *Brachiaria*.[a]

Species and accession	Dry matter (t/ha) when N supply (kg/ha) was:			Crude protein (%) when N supply (kg/ha) was:		
	0	75	150	0	75	150
B. brizantha BRA-000337	5.99 Cc	10.67 Ba	16.83 Aa	7.6	10.6	13.4
B. decumbens BRA-000116	7.82 Ca[b]	10.63 Ba	13.91 Ab	7.5	10.2	13.2
B. decumbens BRA-000141	7.65 Ca	10.35 Ba	10.35 Ab	7.2	10.6	13.4
B. humidicola BRA-000213	6.67 Cb	9.26 Bb	9.26 Ac	6.9	9.0	11.7
B. ruziziensis BRA-000272	7.32 Cab	9.42 Bb	9.42 Ac	7.7	10.5	12.7

a. Values are mean of 2 years with three replications.

b. In each row, means followed by the same capital letter and, in each column, means followed by the same lower-case letter are not significantly different, according to Tukey's test ($P<0.05$).

SOURCES: Alvim et al., 1990; Botrel et al., 1990b.

Associative N_2 fixation. Field experiments in Brazil (Boddey and Dobereiner, 1988; Boddey et al., Ch. 5, this volume) evaluated the contribution of associative N_2 fixation to the N nutrition of *Brachiaria*. Several species were grown in small concrete cylinders or in small plots, using biologically active, uninoculated soils. These experiments provided convincing evidence for significant interspecific differences in natural inputs of biologically fixed N_2 in *Brachiaria* (Boddey and Dobereiner, 1988); estimates ranged from a modest 9% of plant N in *B. ruziziensis* to a substantial 40% in the economically important *B. decumbens*. Extrapolation of small-plot data (Boddey and Victoria, 1986; Miranda and Boddey, 1987) indicated potential N inputs from associative N_2 fixation of 5-10 kg/ha every 30 days during the summer (rainy) season, or 30-40 kg/ha per year. Such estimates of N inputs are consistent with field observations that pure stands of *B. decumbens* in Brazil can remain productive under grazing for many years in the absence of legume N_2 fixation or fertilizer N. However, N_2 fixation is apparently significant only when soil N is deficient (Miranda and Boddey, 1987).

The evidence that *Brachiaria* species can obtain significant proportions of plant N from associative N_2 fixation under natural conditions is unequivocal (Boddey and Dobereiner, 1988). What is less certain is extrapolation from measurements of limited duration on small plots to annual estimates over large areas.

The microbiological aspects of N_2 fixation have not been studied in detail. The identity of the organisms involved has not been established, and little information is available on edaphic factors affecting associative N_2 fixation in tropical grasses. Miranda et al. (1985) showed that *B. decumbens* and the *Azospirillum* associated with this grass responded to applications of Mo. Further investigation is needed of the organisms involved, the conditions that favor associative N_2 fixation (Dobereiner, 1992; Souto and Baldani, 1992; Boddey et al., Ch. 5, this volume), and the magnitude of the effect of host genotype.

Response to shading. Under low N inputs, both *B. brizantha* and *B. miliiformis* (now *B. subquadripara*) have shown higher DM yields and N accumulation when shaded than when

unshaded (Eriksen and Whitney, 1981; Fisher and Kerridge, Ch. 3, this volume). This effect of shading may be related to mineralization being enhanced by increased soil biological activity and/or an alleviation of photoinhibitory effects on photosynthesis of these species.

Adaptation to low phosphorus supply

Phosphorus is the major nutrient limiting the growth and productivity of *Brachiaria* pastures in acid soils (Sánchez and Salinas, 1981). Even soils with a high total P content may have a low capacity to supply P, because of chemical reactions that fix phosphate-P into forms relatively unavailable to plants. The amount of applied P needed to correct a deficiency varies with the P-sorption characteristics of the soil and the ability of the plant to acquire and use P efficiently for plant growth.

At a given P supply, P acquisition by *Brachiaria* species may be improved by (1) a root system that provides greater contact with soil P; (2) a greater uptake per unit root length because of enhanced uptake mechanisms; and/or (3) an ability to use insoluble organic or inorganic forms of P that are generally unavailable or poorly available to plants. Association of vesicular-arbuscular mycorrhizae (VAM) can significantly affect each of these attributes.

Greenhouse studies were carried out at CIAT to determine the plant attributes that enable *B. dictyoneura* cv. Llanero to adapt to low P supply (Rao et al., 1993a; 1995) in two soils of contrasting texture: sandy loam and clay loam. Increase in P

Table 5. Effect of P application level and soil type on shoot growth and plant characteristics of *Brachiaria dictyoneura*.

Plant characteristic	P applied (kg/ha) in:								LSD ($P = 0.05$)
	Sandy loam				Clay loam				
	0	10	20	50	0	10	20	50	
Shoot biomass (g/plant)	0.78	5.44	9.56	13.90	0.24	3.81	8.21	10.35	2.08
Leaf area (m^2/plant)	0.010	0.037	0.072	0.072	0.003	0.027	0.091	0.086	0.024
Root-to-shoot ratio (g:g)	0.66	0.43	0.51	0.54	0.38	0.28	0.36	0.52	0.09
Root length (km/m^2)	2.52	7.94	14.67	17.21	0.75	5.05	11.15	14.24	2.85
Specific root length (m/g)	48.7	33.2	29.6	22.5	80.3	47.6	37.6	25.7	13.7
Leaf-P concentration (g/kg)	0.5	0.6	0.5	0.8	0.6	0.5	0.6	0.8	0.17
P-uptake efficiency (µg/m)	17.0	30.5	27.5	52.9	20.3	37.7	38.9	44.6	12.6
Root acid phosphate (µmol/g fresh wt. per min)	2.95	0.82	0.73	0.24	2.77	1.45	0.78	0.23	0.76
Mycorrhizal infection (% of root length)	64.0	41.7	9.0	1.0	16.0	5.7	10.0	6.3	13.7

SOURCES: Rao et al., 1993a; 1995.

supply (from 0 to 50 kg/ha) increased shoot biomass in both soils (Table 5), but P application was not high enough for an asymptote to be reached. Increased P supply greatly improved leaf expansion and root elongation (Table 5). Leaf P concentrations were relatively unaffected by soil P supply, indicating that P was used efficiently for growth. Phosphorus-uptake efficiency per unit root length (µg/m) increased with the increase in P supply. These data suggest that low P supply limits leaf expansion and root elongation of cv. Llanero.

Although *Brachiaria* species have an abundant fine root system, they are excellent hosts for, and highly dependent on, VAM when grown in low-fertility acid soils (Howeler et al., 1987; Rao et al., 1992; Saif, 1987; Salinas et al., 1985). Soil texture and P supply influence the extent of mycorrhizal infection of roots of cv. Llanero (Table 5). At low P, mycorrhizal infection was less in clay loam than in sandy loam. But specific root length, which is a measure of the extent of fine root production, was greater in clay loam than in sandy loam. Root acid phosphatase activity, an indicator of the use of soil organic P, decreased markedly with increasing P supply (Table 5). *Brachiaria dictyoneura* cv. Llanero can acquire P from less available inorganic (aluminum phosphate) and organic (phytic acid) forms, although in much smaller amounts than can the forage legume, *Arachis pintoi* CIAT 17434 (Rao and Kerridge, 1994).

Inoculation with VAM reduced the external P requirements of *Brachiaria* species by as much as 80% in a tropical acid soil in Brazil (Siqueira, 1987). Saif (1987) evaluated the mycorrhizal dependency (shoot dry weight of mycorrhizal plants expressed as a percentage of shoot dry weight of nonmycorrhizal plants) of 8- to 10-week-old plants of 24 tropical forage grass and legume species, including four species of *Brachiaria*. The mycorrhizal dependency of cv. Basilisk and cv. Marandu was much greater than that of cv. Llanero and cv. Humidícola. Of the four *Brachiaria* species, cv. Marandu, even with VAM inoculation, made the least use of soil P (native soil P + applied P) (Table 6).

Species of VAM show striking differences in their response to soil acidity (Adelman and Morton, 1986). Siqueira et al. (1990) found no evidence for VAM response to lime. However, liming affects VAM populations, depending on the species composition of the original fungal assemblage. Overliming in highly weathered acid soils depresses plant growth, but this is attributed to reduced P uptake, resulting from dicalcium phosphate precipitation and induced trace element deficiencies (Siqueira et al., 1990).

Table 6. Effects of vesicular-arbuscular mycorrhizal (VAM) inoculation on dry matter yield and percentage of P used in the soil by different *Brachiaria* species grown in sterilized Oxisol (M = inoculated; NM = not inoculated).

Species	Shoot dry weight (g/pot)		Root dry weight (g/pot)		Percentage of P used in the soil[a]	
	M	NM	M	NM	M	NM
B. brizantha cv. Marandu	4.84	0.30	2.07	0.18	17.3	1.6
B. decumbens cv. Basilisk	4.68	0.28	2.57	0.21	24.8	1.6
B. dictyoneura cv. Llanero	4.92	0.91	2.56	0.46	25.3	4.7
B. humidicola cv. Humidícola	5.19	1.27	2.82	0.85	27.8	7.1

a. Percentage use of soil P = $\frac{\text{Total P absorption}}{\text{Applied P}}$ x 100

SOURCE: Saif, 1987.

The research reviewed here indicates that *Brachiaria* species (particularly *B. dictyoneura* cv. Llanero) respond to an increased P supply in terms of both shoot and root growth. Their main strategy for acquiring P from fertilizer applied to acid soils appears to be the production of an extensive root system, together with VAM fungal association, to explore a greater volume of soil (Rao et al., 1993a).

Adaptation to low calcium supply

In low-fertility acid soils, plant growth can be limited by Ca deficiency. Many subsoils have less than 0.1 $cmol_c$ Ca/kg of soil (= 20 mg Ca/kg). Because Ca is not mobile in the phloem, it does not move downward in the roots toward the root tips, where it is required for growth. Thus, root tips have to meet their Ca demand for growth by direct uptake from their environment.

Recent field experiments with *Brachiaria* species grown on Oxisols in the Colombian Llanos support this view of Ca limitation. Calcium application increased shoot DM production, both lime and gypsum giving similar increases, although only lime increased soil pH (K. Häussler and I. M. Rao, unpublished data). This work has shown higher Ca acquisition in *B. ruziziensis* than in *B. dictyoneura* cv. Llanero, with Ca concentrations twice as high in the shoot DM and three times as high in uptake of Ca by the above-ground biomass (K. Häussler and I. M. Rao, unpublished data). This efficiency in Ca acquisition is related to the extensively branched root system of *B. ruziziensis*; that is, it has numerous root tips, which are the main sites of Ca uptake along the root axis (Häussling et al., 1988; Marschner and Richter, 1974).

Other field experiments conducted on an Oxisol of the Colombian Llanos have shown considerable interspecific variation in Ca requirements (CIAT, 1981). *Brachiaria humidicola* has lower external Ca requirements (50 kg Ca/ha, only 125 kg $CaCO_3$/ha), and lower internal Ca requirements (0.22% Ca in DM) than *B. decumbens* (0.37%) or *B. brizantha* (0.37%).

Greenhouse studies using Oxisols of contrasting texture (clay loam and sandy loam), also indicated marked interspecific differences in Ca acquisition and internal use among four *Brachiaria* species (Table 3; I. M. Rao, unpublished data). Although cv. Basilisk and cv. Marandu acquired more Ca, cv. Humidícola and cv. Llanero used Ca for growth much more efficiently. The significance of this variation in acquisition and use of Ca requires further investigation.

Screening procedures to assess adaptation to acid soils

The classical method of screening for tolerance of low-fertility, acid soils is based on forage yield responses. However, because this is very expensive, we need indirect parameters, based on the physiological responses of plants to the soils on which they are grown. Such parameters need to be easy to measure, and the procedure must enable quick screening of large plant populations.

Plant growth in low-fertility acid soils is not often limited directly by H^+ activity, but rather by Al or Mn toxicity and/or deficiency of essential nutrients, such as N, P, or Ca (Foy, 1992). Fernandes et al. (1984) tested the effects of Al levels (0, 0.75, 1.5, 3, or 6 mg/L) in nutrient solution on *B. decumbens* (Al-tolerant) and *Cenchrus ciliaris* (Al-sensitive). They found no differences in root elongation between the two grasses, but *C. ciliaris* showed a reduction in root volume as Al levels in the solution increased. In *B. decumbens*, a positive correlation was found between root cation exchange capacity (CEC) and Ca accumulation and a negative correlation between CEC and K and Al accumulation. No such correlations were found in *C. ciliaris*. The authors suggested that in *B. decumbens*, the blocking of CEC sites by Al favors K uptake over Ca uptake.

Differences in Mn tolerance of several *Brachiaria* species and accessions were tested at Quilichao, Colombia, using the natural distribution of soil Mn from low (0-20 mg/kg) to high (>50 mg/kg) in a field experiment (CIAT, 1981; J. G. Salinas, unpublished data). Differences were greater at the accession than at the species level; the most Mn-tolerant accessions (*B. decumbens* cv. Basilisk, *B. brizantha* CIAT 665, and *B. ruziziensis* CIAT 654) produced more DM at high than at low Mn levels, which indicates a beneficial, rather than a detrimental, effect of Mn.

A seedling-based bioassay was developed (CIAT, 1993) to screen *Brachiaria* species for acid-soil tolerance. Because root elongation is very sensitive to Al in soil solution, root length density (RLD) was measured as a function of exchangeable Al in the soil for *B. decumbens*, *B. brizantha*, and *B. ruziziensis*. *Brachiaria decumbens* is much more persistent on acid soils than the other two species. However, increase in exchangeable Al in soil reduced RLD of all three species in a similar manner (Figure 1). This indicates that the differences in adaptation cannot be attributed to Al toxicity.

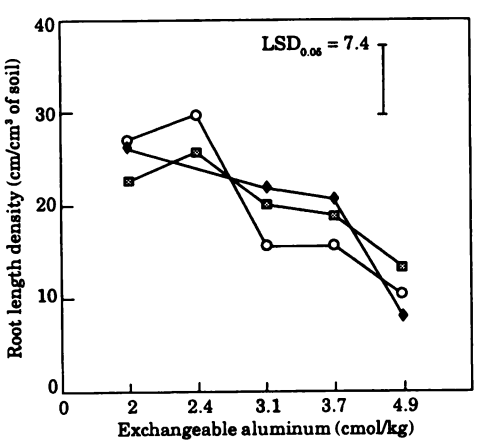

Figure 1. Root length density per unit soil volume of three *Brachiaria* species (○ = *B. decumbens*, ♦ = *B. brizantha*, and ⊠ = *B. ruziziensis*) as affected by exchangeable Al in a clay loam.

Nutrient Requirements

Knowledge of the specific nutritional requirements of different *Brachiaria* species can help determine more precisely the amount of fertilizer needed to establish pastures rapidly and maintain productivity over time.

Satisfaction of the nutrient requirements of *Brachiaria* species depends on several factors, which differ with ecotype and soil type (Malavolta and Paulino, 1991; Paulino et al., 1987). The availability of a nutrient in the soil solution differs with the total amount of the nutrient present, and with its distribution between the soil solution and the adsorbed forms. The internal (plant) nutrient requirement is the concentration in the plant when growth is no longer constrained by the nutrient in question; it is usually defined in terms of a critical concentration. The external (soil) nutrient requirement is similarly some measure of the concentration in the soil, or preferably the soil solution. The critical concentration, both in the plant and in the soil, is considered as that required to obtain 80% of the maximum production (Salinas and Saif, 1990).

Table 7 shows critical values of internal P, K, Ca, and S in foliar tissue of three *Brachiaria* accessions, compared with *Andropogon gayanus* and *Panicum maximum*. Internal P and Ca requirements for plant growth of the *Brachiaria* species are much lower than those of *P. maximum*. *Brachiaria humidicola* appears to require lower internal concentrations of P, K, and Ca than the other two *Brachiaria* species. When grown on a low-fertility Latosol in Brazil, *B. brizantha* had a much higher external P requirement (10.8 mg/kg Mehlich-1 P and 21.8 mg/kg resin P) than *B. decumbens* (4.7 and 10.7 mg/kg) (Correa, 1991).

Competition for soil nutrients is a key factor in the stability and persistence of grass-legume associations under grazing (Haynes, 1980). In particular,

Table 7. Critical levels for internal P, K, Ca, and S for five forage species.

Species	Plant concentration (% of dry weight)			
	P	K	Ca	S
Andropogon gayanus	0.10	0.95	0.23	0.15
Brachiaria brizantha	0.09	0.82	0.37	-
B. decumbens	0.10	0.83	0.37	0.16
B. humidicola	0.08	0.74	0.21	0.14
Panicum maximum	0.17	-	0.60	0.15
Animal requirements	> 0.12	> 0.60	> 0.18	> 0.10

SOURCE: CIAT, 1981; J. G. Salinas, unpublished data.

grasses are more efficient than legumes in acquiring K from the soil; however, this efficiency decreases as the supply of K to soil increases through fertilizer application. This differential ability of grasses and legumes to acquire K was found to be strongly associated with the CEC of their roots (CEC_r). In general, the CEC_r of legumes was found to be higher than that of grasses, which may contribute to greater divalent cation (Ca, Mg) absorption by legumes (CIAT, [1984]). In contrast, grasses may acquire larger amounts of monovalent cations (K, Na) than legumes. These differences in CEC_r and cation acquisition rates between grasses and legumes can therefore influence their stability and dominance when grown in associations. Thus, the more nearly equal the CEC_r of the grass and legume growing in association, the more compatible the mixture will be in acquisition of nutrient cations (J. G. Salinas, unpublished data).

Diagnosis of Nutrient Disorders

Fertilizer deficiencies can be diagnosed by two major methods: (1) visual observation of plant growth and identifiable deficiency symptoms; and (2) chemical analysis: (a) soil testing for pH, exchangeable Al, and available nutrients, and (b) plant analysis for nutrient concentrations.

Visual diagnosis

A normal dark green color characterizes a good nutrient supply, but any change to light green or yellowish tinges suggests a deficiency, provided other factors, such as extreme temperatures, diseases, spray damage, or air pollution, are not responsible. The easiest way to diagnose is to identify deficiency/toxicity symptoms from a color photograph (Figure 2; Table 8). However, the precise cause may not be easy to establish from observation alone, particularly in cases of latent deficiency ("hidden hunger"), for which chemical methods will usually be needed.

Chemical diagnosis

The main limitation to soil testing lies in selecting and calibrating relevant extraction methods for particular soil types and plant species. The choice of a suitable method requires calibration in one of three ways: (1) field experiments, in which the relative forage yield with and without fertilizer is correlated with the relative extraction data from soil with and without fertilizer (r^2 should be at least 0.6 and preferably >0.7); (2) plant nutrient concentration, in which the nutrient concentration in the plant at a particular growth stage is correlated with the nutrient extraction data from the soil (less expensive and less effective but still useful); (3) appearance of deficiency symptoms, comparing the nutrient extraction data from the soil with the appearance or nonappearance of symptoms (useful for approximate classification of micronutrients).

Plant analysis based on nutrient concentrations in plants provides reliable

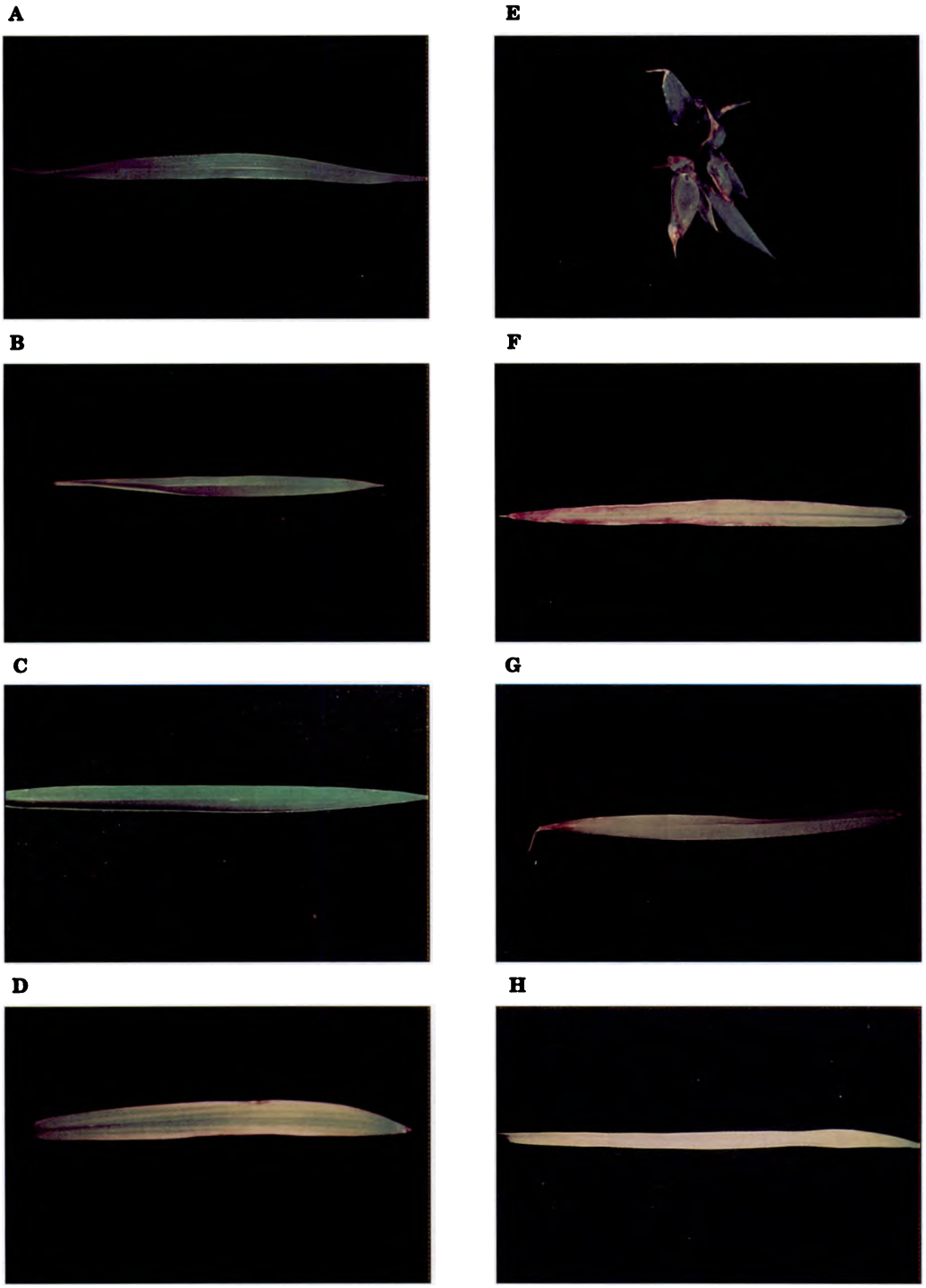

Figure 2. Visual symptoms of nutrient disorders in leaves of *Brachiaria decumbens* CIAT 606: (A) control; (B) N deficiency; (C) P deficiency; (D) K deficiency; (E) Ca deficiency; (F) Mg deficiency; (G) S deficiency; and (H) Zn deficiency.

Table 8. Key to nutrient deficiency symptoms in *Brachiaria* species.

Symptom	Deficiency
Symptoms appearing first on **older** leaves:	
Chlorosis starting from leaf tips	N
Necrosis on leaf margins	K
Chlorosis mainly between veins (which remain green)	Mg
Brownish, grayish, whitish spots	Mn
Reddish color on green leaves or stem	P
Symptoms appearing first on **younger** leaves:	
Tip-burn, serrated leaf edge	Ca
Mottled yellow-green leaves with yellowish veins	S
Mottled yellow-green leaves with green vein	Fe
Young leaf with white tip	Cu
Youngest leaf brownish or dead	B

information on their nutritional status at the date of sampling, thereby providing a guide for maintenance fertilization. Interpretation is usually based on the total concentration of nutrients in leaves or in tops, compared with previously determined critical nutrient concentrations, or critical values.

The external and internal critical values suggested for *A. gayanus*, based on general information for tropical forage grasses, may serve as a guide for *Brachiaria* species (Salinas and Saif, 1990).

Response to Liming and Fertilization

Spain (1979) evaluated the response to lime of four *Brachiaria* species (*B. decumbens*, *B. humidicola*, *B. radicans* [now *B. arrecta*], and *B. mutica*) in a field trial on an Oxisol in the Colombian Llanos. He applied 0, 0.5, 2, or 6 t/ha of lime, which gave Al-saturation levels of approximately 90%, 85%, 60%, and 15%, respectively. All four species showed excellent tolerance of Al, and all reached near-maximum DM yields with lime application rates of 0-0.5 t/ha. At Chipiriri, Bolivia, *B. decumbens* showed no response and *B. brizantha* only a minor (27%) response to lime (Vallejos A., 1986). In an association of *B. decumbens* and *Pueraria phaseoloides* on an Ultisol in Bahia, Brazil, neither species responded to lime during establishment (Cantarutti, 1990).

Several field and greenhouse studies were conducted in Brazil to evaluate the interaction of lime and P fertilizer applied to *B. decumbens* and *B. humidicola* (Costa et al., 1990; Echeverría et al., 1982; Paulino, 1986). These trials demonstrated a marked response to P application, but almost no response to liming, which may be because soil Ca was adequate for plant growth. A greenhouse study at Campo Grande, Brazil, compared shoot and root growth of *B. decumbens* and three accessions of *B. brizantha* grown on an Oxisol, when fertilized with lime and P. Shoot and root growth showed a marked response to P application, but no response to lime when P supply was adequate (Table 9). When P supply was low, application of high rates of lime improved growth, probably because of an increase in N supply through enhanced mineralization in the soil (J. C. Almeida and M. C. M. Macedo, unpublished data).

The residual effects of three rates of lime and five sources of P were evaluated on an established pasture of *B. decumbens* for 10 years on a Latosol of the Brazilian Cerrados (Sanzonowicz et al., 1987). The residual effect of all sources of P at higher levels was greater than that of lime. Application of lime was said to improve response to natural rock phosphate.

Table 9. Influence of lime and P fertilizer on plant growth characteristics of *Brachiaria* species and *Andropogon gayanus*.

Plant characteristic	Lime rate (t/ha)[a]	P rate (kg/ha)[b]	Species and accession[c]				
			B. decumbens	*B. brizantha*			*A. gayanus*
				Marandu	B 166	B 178	
Shoot biomass (g/pot)	1	0	2.3	3.5	1.2	4.6	4.2
		140	34.4	29.7	35.5	38.5	25.2
	4	0	5.3	7.6	2.8	7.9	5.5
		140	33.8	32.2	34.4	36.7	22.0
Root biomass (g/pot)	1	0	0.4	0.9	0.2	1.0	3.3
		140	10.5	9.7	7.4	11.7	8.9
	4	0	2.0	2.3	0.7	2.1	3.1
		140	8.9	9.1	4.9	10.2	7.7
Root-to-shoot ratio (g:g)	1	0	0.17	0.25	0.17	0.21	0.79
		140	0.30	0.33	0.21	0.30	0.35
	4	0	0.56	0.30	0.25	0.27	0.56
		140	0.35	0.28	0.14	0.28	0.35

a. Base saturation at harvest: 22% at 1 t/ha and 55% at 4 t/ha.

b. Soil P level (Mehlich-1): 2 mg/kg at 0 kg/ha and 10 mg/kg at 140 kg/ha.

c. Species differ significantly, according to the F test ($P<0.01$).

SOURCE: J. C. Almeida and M. C. M. Macedo, unpublished data.

Subsequent experiments on Oxisols in Brazil failed to confirm these observations.

Nutrient Composition and Forage Quality

The influence of amount and availability of mineral nutrients on forage quality of tropical grasses has been extensively reviewed (Minson, 1990). Fertilizer application can have both direct and indirect effects on animal production by inducing chemical, morphological, or physiological changes in plants. Nutrient composition of forage can be important in preventing livestock diseases, as well as in stimulating or inhibiting ruminal microbial activity.

Although *Brachiaria* species are widely grown, their forage quality is often low, largely because of the low N, P, Ca, and S status of the soils on which the grasses are grown. Supply of N fertilizer or introduction of forage legumes can improve the quality of *Brachiaria* species, but deficiency of other nutrients still limits forage quality on acid soils. Furthermore, large areas will remain under pure grass pastures without the benefit of N inputs. Little attention has been focused on maintaining forage quality over time. Environmental conditions in the tropics favor rapid growth, accompanied by a high proportion of stem, high fiber concentration (reduced nonstructural carbohydrates), and reduced digestibility. Higher forage quality leads to higher intake and digestibility, which contribute to improved animal performance. The interaction of soil fertility with forage quality of *Brachiaria* species needs to be investigated further.

Fertilizer Management

The response of different *Brachiaria* species to applied N, P, K, Ca, Mg, S, and micronutrients has been extensively reviewed (Malavolta and Paulino, 1991; Paulino et al., 1987; Salinas and Saif, 1990). In general, responses to P and S

were more common than responses to other nutrients (Malavolta and Paulino, 1991). Salinas and Saif (1990) reported that *B. decumbens* CIAT 606 responded more to N than *A. gayanus* CIAT 621 in terms of DM production and N recovery from the soil. Comparative studies on the effects of available P and percentage of Al saturation on yields of four forage grasses (*B. humidicola*, *A. gayanus*, *D. decumbens* [now *D. eriantha*], and *P. maximum*) on an Oxisol in the Colombian Llanos indicated that *B. humidicola* and *A. gayanus* were the most efficient grasses at low P, as they produced 80% of maximum yield with minimum reduction in Al saturation (Salinas and Saif, 1990). Dias Filho (1992) found that, per unit of forage produced, partially acidulated rock phosphate (PARP) was less economical than single superphosphate (SSP) applied to *B. brizantha* cv. Marandu on a forest soil of the Brazilian Amazonian region. This study indicated that the soluble P fraction in PARP may be a better indicator of agronomic and economic efficiency than total P.

Response to K, S, and Ca fertilizer applications was greater for *B. decumbens* than for *B. humidicola* (Salinas and Saif, 1990). The response to S was greater in the Brazilian Cerrados than in the Colombian Llanos (Malavolta and Paulino, 1991; Salinas and Saif, 1990). No clear response to Mg was recorded, except with small amounts of dolomitic lime, which meet the requirements of both Ca and Mg. Responses of *Brachiaria* and *A. gayanus* to micronutrients (Zn, Cu, B, and Mn) were negligible (CIAT, 1985; J. G. Salinas, unpublished data). This lack of response may be because the forage species are efficient in acquiring the micronutrients from the low reserves in acid soils and/or in using them for plant growth.

Maintenance fertilizer requirements of *Brachiaria* species appear to be low in the Colombian Llanos. Pure grass pastures of *B. decumbens* as well as associations of *B. decumbens* + *P. phaseoloides* have continued to give high animal production over 16 years, with only small amounts of maintenance fertilizer (in kg/ha: 10 P, 9 K, 92 Ca, 8 Mg, and 11 S) every 2 years (Lascano and Euclides, Ch. 7, this volume).

Conclusions

Several commercially grown *Brachiaria* species are well adapted to low-fertility, acid soils of the tropics. Research to identify plant attributes that contribute to efficient acquisition and use of nutrients for plant growth is recent. Several root and shoot attributes have been shown to contribute to the adaptation of *Brachiaria* species to acid soils; these include their ability to change the partitioning of fixed carbon to favor root growth, to acquire N through associative fixation, to acquire P through extensive root systems and mycorrhizal association, and to acquire Ca through highly branched root systems. Differences in adaptation to acid soils among *Brachiaria* species cannot be attributed to Al toxicity. Internal requirements of P, Ca, and K for growth of *B. humidicola* are much lower than those for other species. Greenhouse and field studies have demonstrated striking responses in forage yield to P, but no response to lime nor to micronutrient applications. Rapid and reliable screening procedures are urgently needed to improve the efficiency of evaluation and genetic improvement of *Brachiaria* germplasm.

Future Research Priorities

The following aspects of edaphic adaptation of *Brachiaria* require more research attention, preferably through collaboration between plant nutritionists, animal nutritionists, and soil fertility agronomists:

1. Screening procedures to assess edaphic adaptation.
2. Identification of plant attributes that enhance nutrient acquisition in infertile acid soils.

3. Role of associative N_2 fixation and its relationship to edaphic adaptation.
4. Role of VAM in nutrient acquisition and carbon partitioning.
5. Identification of genotypes with greater nutrient acquisition and forage quality.
6. Relationships between soil-plant nutrient status and forage quality.
7. Competition for nutrients in mixed systems.

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To save space, the following acronyms are used in place of publishers' names:

INIAA = Instituto Nacional de Investigación Agraria y Agroindustrial

IVITA = Instituto Veterinario de Investigaciones Tropicales y de Altura

SBZ = Sociedade Brasileira de Zootecnia

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Chapter 5

Nutrient Cycling and Environmental Impact of *Brachiaria* Pastures

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Abstract

Since the 1960s, 50-70 million hectares of native savannas in tropical America have been planted with pastures of introduced *Brachiaria* species. Recently, productivity has declined over much of this area for several reasons, a major one of which is the immobilization of plant-available nitrogen by large quantities of grass litter of very high C-to-N ratio. For the extensive beef cattle pastures of tropical America, N fertilization is usually not economical, and legumes have been introduced to provide biologically fixed N. The plant litter of mixed grass-legume swards contains more N, thus decreasing the C-to-N ratio and favoring pasture sustainability, according to studies in Brazil and Colombia.

These studies also suggest that the environmental impact of a vigorously growing *Brachiaria* pasture is only positive: the grass provides good soil cover, facilitating water infiltration and preventing erosion; leaching of soluble nutrients is minimal; N_2 fixation associated with some *Brachiaria* genotypes may slow down pasture decline; and the grass's deep, dense rooting system also sequesters much more atmospheric C than native pasture. The large area occupied by *Brachiaria* pastures suggests that this may be a sink of global significance for atmospheric CO_2.

Sustaining the productivity of pastures while improving animal production requires strategies for maintaining or even improving soil fertility. One effective strategy is to introduce forage legumes.

Introduction

Savannas occupy about 250 million hectares of South America, mainly in Brazil (200 million), Venezuela (28 million), and Colombia (20 million). Over half of this area is used for extensive cattle ranching, of which about 40 million hectares are improved pastures, planted mainly to *Brachiaria* species and some *Andropogon gayanus* (about 7 million hectares: Vera et al., 1992). The substitution of native vegetation on such a large scale with these African grasses is bound to have both local impact on soil fertility and composition and regional impact on the hydric balance and water quality. It may even influence the emission or sequestration of gases that affect the global environment.

The study of nutrient cycling in these pasture systems can help us evaluate the magnitude of these impacts, and determine the effects of management strategies on pasture productivity and sustainability. In this paper, we review the information on nutrient (principally N) cycling in such pastures; the effects of different animal management options, forage legumes, and P fertilization on pasture sustainability; and the environmental impact of transforming native vegetation, whether savanna or forest, to improved pastures in South America.

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Sustainability and Nutrient Cycling in *Brachiaria* Pastures

Most improved pastures in the South American savannas have been established within the last 30 years. In almost all areas, initial establishment of the grass requires inputs of P, lime, and trace elements. Once these nutrient deficiencies have been corrected, good pasture productivity—animal liveweight gains (LWG) of 100-300 kg/ha per year are typical (Lascano, 1992)—can be maintained for several years, with only modest inputs of phosphatic and/or potassic fertilizers.

In these low-fertility acid soils, P deficiency is almost universal, but addition of P fertilizer (superphosphate or sometimes rock phosphate) is usually economically viable. This is particularly so when the P, along with K and lime, are added to pioneer crops such as rice or maize, which give a much higher economic return than beef production, and the subsequently established pastures benefit from the residual effect of this fertilization (Rao et al., 1993; Thomas et al., 1995; Vera et al., 1992).

Well-adapted, well-managed pastures of *Brachiaria*, particularly in association with forage legumes, have low levels of soil nutrient extraction, because most of the output is high-quality energy and protein that is primarily made up of freely available atmospheric C, N, H, and O, and only small amounts of P, K, Ca, and Mg from the soil. Such pasture systems also maintain high above-ground production and profuse, vigorous root systems, which minimize nutrient leaching and soil erosion while improving soil biological activity, structure, and fertility (Rao et al., 1992; 1994; Thomas et al., 1992; 1995).

Export of nutrients from the soil-plant-animal system in animal products is low in such pastures, as 80%-90% of nutrients consumed by the animals are returned to the pasture in the form of urine and feces. Beef cattle carcasses contain about 2.5% N, 0.8% P, and 0.2% K (CAB, 1980; Maynard et al., 1979), so that even a productive tropical pasture yielding 300 kg/ha per year of animal LWG would only lose 7.5 kg N, 2.4 kg P, and 0.6 kg K/ha by this route.

Phosphate is well conserved in these soils. Because of its low solubility in acid soils, leaching losses are minimal. Potassium losses, mainly through animal urine, can be more significant. A study on K cycling performed on a grazed pasture of *Desmodium ovalifolium* and *B. humidicola* in Yurimaguas, Peru, indicated annual losses of about 30 kg/ha K via leaching from urine patches (Ayarza, 1988). Nitrogen loss can be even more significant, because N is more concentrated in animal excretions than P or K, and because N can also be lost to the atmosphere via ammonia volatilization or, in poorly drained soils, by denitrification, as well as by leaching.

Losses of mineral nutrients released by mineralization of plant residues (litter and decaying roots) are generally small in a productive pasture, as release is gradual, and the dense layer of active roots captures soluble nutrients efficiently. Some leaching losses, such as those experienced in the central region of the Brazilian Cerrados, may occur after a severe dry season, when considerable mineralization takes place at the start of the rains, before new root growth begins.

In summary, grass pastures apparently fulfill an important prerequisite for agrosystem sustainability, namely conservation of nutrients—except possibly N—in the soil-plant-animal system (Sánchez and Ara, 1991). However, in both the tropical (mainly *Panicum maximum*) pastures of Queensland, Australia (Graham et al., 1981; Robbins et al., 1989), and the *Brachiaria* pastures of the savannas and forest margins of South America (Barcellos, 1986; Buschbacher et al., 1988; Cantarutti, 1985; Carvalho et al., 1990; Moya, 1991; Serrão and Dias Filho, 1991;

Serrão et al., 1979; Spain and Gualdrón, 1991; Argel and Keller-Grein, Ch. 14, this volume; Pizarro et al., Ch. 15, this volume), experience has shown that, after some years, grass and animal productivity decreases, and pasture degradation sets in. The symptoms of this decline are sparse soil cover by the grasses, soil compaction, invasion by species of low productivity and palatability, and the appearance of many termite mounds.

The main cause of this decline in productivity is thought to be the lack of available mineral N for adequate plant growth (Myers and Robbins, 1991; Spain and Gualdrón, 1991). *Brachiaria* and *Andropogon* species deposit large quantities of litter and decaying roots of very low N content (0.5%-1.0% N), and although this increases soil organic matter (OM), the high C-to-N ratio of this material produces a large soil microbial biomass that is deficient in N and competes effectively with plants for available mineral N (Robertson et al., 1993a; 1993b). Hence, in permanent pastures, N usually becomes the primary factor limiting pasture productivity. Application of fertilizer N can correct this deficiency, but its effect—unlike that of P or K fertilizers—lasts only 1-2 months, and applications must be repeated regularly, which is not economically viable for most beef cattle production systems in South America. In view of the key role of N in the sustainability of these improved pastures, several recent studies in Brazil and Colombia have focused on N cycling in these systems.

Nitrogen Cycling in *Brachiaria* Pastures

The N cycle—like that of any nutrient—can be separated into gains to, losses from, and cycling within, the soil-plant-animal system. Gains to the system are restricted to N from atmospheric and rainfall deposition, which are generally regarded as insignificant, and from biological N_2 fixation (BNF). When legumes are introduced into the pasture, they are usually capable of obtaining more than 80% of their N from BNF (Vallis et al., 1977), unless the efficiency of the N_2-fixing symbiosis is restricted by deficiency of P, K, or micronutrients (Cadisch et al., 1989). The contribution of BNF to the pasture from the legume depends on the total dry matter (DM) production, the proportion of legume in the sward, and the proportion of legume N derived from BNF (Cadisch et al., 1994a; Thomas, 1992).

In a recent study at EMBRAPA's Centro de Pesquisa Agropecuária dos Cerrados (CPAC) near Brasília, total DM production (including litter) of a sward of *A. gayanus-Stylosanthes* species was estimated to be 10-17 t/ha per year, of which 32%-48% was legume material (Cadisch et al., 1994b). A ^{15}N-dilution satellite experiment gave a mean estimate of 81% of legume N derived from BNF, corresponding to an input of 67-117 kg/ha per year of N to the system. Similarly, in three grass-legume pastures (*B. dictyoneura* CIAT 6133[1] with *Arachis pintoi* CIAT 17434, or *Centrosema acutifolium* cv. Vichada, or *S. capitata* cv. Capica) established with two rates of fertilization on an Oxisol in Colombia, the proportion of legume N derived from fixation averaged 89% over 2 years (Thomas and Asakawa, 1993b) and was not significantly different in the third year (R. J. Thomas, unpublished data).

The ^{15}N-dilution studies done on small plots (60-cm-diameter cylinders) at EMBRAPA's Centro Nacional de Pesquisa de Agrobiologia (CNPAB) suggest that *Brachiaria* species may be able to obtain significant, although more modest, contributions from BNF (Boddey and Victoria, 1986). These data suggest that *B. decumbens* and *B. humidicola* may be able to obtain as much as 5-7 kg/ha per month from plant-associated BNF in the warm, moist periods of the year (Figure 1). Differences among *Brachiaria* species in their susceptibility to pasture

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

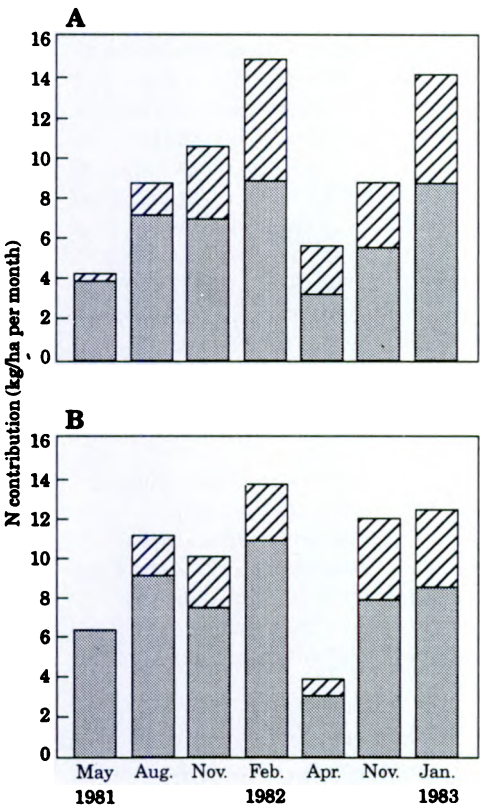

Figure 1. Estimated contribution of biological N_2 fixation (BNF) to the nutrition of (A) *Brachiaria decumbens* and (B) *B. humidicola* grown in concrete cylinders (60-cm diameter), filled with ^{15}N-labeled soil. ▩ = soil N; ▨ = N from BNF. (After Boddey and Victoria, 1986.)

decline may be due to differences in their capacity to obtain N from BNF. More studies are required on different species and genotypes of *Brachiaria*, and on the contribution of such BNF inputs under field conditions.

As mentioned above, losses of N from the pasture system are probably restricted mainly to losses from the high concentrations in animal excreta. Most N in animal urine is in the form of urea, with smaller quantities of ammonium and amino acids. Urea can be quickly hydrolyzed to ammonia by soil urease activity and subsequently lost by volatilization, or leached as ammonium or, after nitrification, as nitrate. If nitrate levels are significant and soil drainage is restricted, causing anaerobic zones in the soil, much of the NO_3^--N can be lost as N_2O or N_2 via denitrification.

Cattle fed on diets rich in protein excrete more N in urine than in dung (Henzell and Ross, 1973), thus total N losses are greater from pastures with high-protein herbage. In contrast, when cattle are fed low-protein diets, such as those obtained from grazing *Brachiaria*, which typically contains 7%-11% protein (Böhnert et al., 1986; Pereira et al., 1992b), they excrete about equal amounts of N in urine and dung. The N in dung is largely organic, and only 20%-25% is water soluble (Haynes and Williams, 1993), hence total N losses are much smaller in low-protein pastures.

A study was done at CNPAB to quantify losses of N from cattle dung. Pats of dung placed in perforated plastic trays on top of 5 cm of soil lost only 10% of their total N over a period of 93 days (E. Ferreira, S. Urquiaga, and R. M. Boddey, unpublished data). After the first 4 days (during which there was no rainfall, and daytime temperatures reached 26-27 °C), a hard crust formed on the dung; even 25 mm of rainfall on the 23rd day did not break this crust. Most N loss occurred in the first 5 days, when NH_4^+ levels in the dung fell from 700 to 60 μg N/g of dry dung. These data suggest that N losses from cattle dung are minor, even at high temperatures; however, the fate of N in the dung is not known for many tropical pastures.

Most studies on N losses through urine have been performed under temperate conditions (Haynes and Williams, 1993). They show that ammonia volatilization losses are favored by high temperatures and wind velocity, and open spaces in the sward. Leaching losses are favored by high rainfall, low soil cation exchange capacity (CEC), and low water-holding capacity (WHC). Losses of N from urine under tropical and subtropical conditions are probably

considerably higher than under temperate conditions, where temperatures are lower and soil CEC and WHC usually higher. Studies performed in tropical Queensland show that 15%-50% of urine N can be lost under these conditions (Vallis et al., 1982; 1985). Recent evidence from ^{15}N-labeled cattle urine applied to a pasture of *B. dictyoneura* cv. Llanero, sown on an Oxisol in Colombia, indicated a subsequent recovery of urine-N by plants of only 10% (R. J. Thomas and M. Rondón, unpublished data).

Effect of phosphorus on nitrogen supply

Few studies have been conducted on the cycling of N within the soil-plant-animal system in *Brachiaria* pastures, but two recent studies in Brazil have shown the effect of P fertilization on these processes.

One study was done near Campo Grande, Mato Grosso do Sul, on a grazed pasture of *B. decumbens*, grown on a quartzitic sand that is typical of about 30% of the Cerrados soils in this Brazilian state (pH 4.8, available P 3.8 mg/kg, 80% Al^{3+} saturation). Phosphorus fertilization increased grass DM production and animal weight gain; the N content of the green leaves also increased from 1.4% to 2.3%, but P concentration (0.14%) was unaffected (Schunke et al., 1991). This suggested that P fertilization stimulated N turnover. Therefore, a subsequent investigation was undertaken at the same site (Schunke et al., 1992).

A uniform 16-ha paddock of *B. decumbens* was divided into two equal areas; one half received 44 kg/ha P as single superphosphate. Both pastures were grazed from November 1991 to November 1992 by Nelore cattle, the P-fertilized paddock by 14 animals (1.75 head/ha) and the unfertilized one by 11 animals (1.38 hd/ha). For the first 5 months of the study (wet season, November-April), animal weight gain averaged 660 g/day on the unfertilized paddock and 920 g/day (40% higher) on the P-fertilized one.

Total DM productivity per year (standing material + litter, estimated in areas protected from grazing) was 12.9 t/ha for the P-fertilized paddock, and 9.7 t/ha for the other, although the concentration of N in the plant material was not affected by P fertilization. The total deposition of litter (estimated from fixed quadrats) in the pastures was 30% higher in the P-fertilized paddock, even though the N content of the litter was lower (0.63% versus 0.82% in the unfertilized paddock). The total N recycled in the pasture was almost equal in both paddocks, at 38 kg/ha.

The conclusion from this study is that P fertilization of this acid, nutrient-deficient soil increased the production of *Brachiaria* and the weight gain of the grazing animals, without diminishing the N recycled in the litter. Pasture sustainability was therefore not prejudiced.

Effect of stocking rate and legume association

In the extreme south of Bahia State, Brazil (16°39' S, 39°30' W), in the forested area of the Atlantic coastal region, a study was conducted to evaluate the effect of animal stocking rate and the introduction of a legume on N cycling in a *B. humidicola* pasture. Mean rainfall in this area is 1,300 mm, with no marked dry season, and temperatures range from 19 to 29 °C. Much of this area has been deforested over the last 20 to 30 years, and the soil (Tabuleira type) at the site (CEPLAC's Estação de Zootecnia do Extremo Sul da Bahia [ESSUL]) is a Haplorthox (pH 4.3, available P 1 mg/kg, Al^{3+} saturation 50%), with the top 40 cm containing 73%-83% sand.

The experiment was originally installed in 1987 with three pastures: (1) *B. humidicola* monoculture, (2) *B. humidicola/D. ovalifolium*, and (3) *B. humidicola/Pueraria phaseoloides* (kudzu). Three stocking rates were used: nominally 2, 3, and 4 hd/ha, with three replicates (paddock size 0.75-1.33 ha). Grazing started in March 1988 (Pereira et

al., 1992a; 1992b). After 1990, the kudzu did not persist, hence the third treatment (data not presented here) was pure grass, fertilized with 4 x 50 kg N/ha per year.

Daily animal weight gains ranged from 850 to 1,512 g/ha in the first year. After 4 years of almost continuous grazing, animal performance declined somewhat, this effect being more marked in the pure grass than in the grass-legume sward (Table 1).

From June 1992 to June 1993, measurements of litter deposition and existing litter were made on fixed and random quadrats (0.5 x 1.0 m), respectively. The year's total deposition was 14.7-17.0 t/ha, and was only marginally affected by animal stocking rate (Figure 2A) or the presence of the legume (Figure 2C). However, the N content of the litter was considerably higher in the grass-legume pasture (Figure 2D) than in the pure grass (Figure 2B), especially at the two lower stocking rates. Neither total DM production nor animal consumption was evaluated during this period. However, animal consumption was evaluated, on three occasions during the initial study (March 1988-March 1989), with the chromic oxide technique (Corbett, 1981), when animal weight gain was 49% higher on the pure grass and 37% higher on the grass-legume sward (stocking rate 3 hd/ha, Table 1), than in 1992-1993. Mean animal intake during this 12-month period was estimated at 9.1 and 6.2 t/ha, respectively (Pereira, 1991). Correcting this for the lower animal weight gain, animal intake was estimated at 6.1 and 4.5 t/ha, and N consumption at 82 and 90 kg N, for the pure grass and mixed pasture, respectively.

This suggests that pasture utilization was about 28% of DM in the pure grass pasture and 24% in the mixed pasture, within the range indicated for such pastures by Wetselaar and Ganry (1982), and close to the value of 30% used in simulations by Thomas (1992). The N utilization for the pastures was estimated to be higher, at 42% for the pure grass pasture and 37% for the mixed pasture, reflecting the selection by the grazing animals of material richer in protein, which was demonstrated by Pereira et al. (1992b) in this pasture, and which has also been demonstrated by other authors in studies on other mixed *Brachiaria*-legume pastures (Böhnert et al., 1986; Cárdenas and Lascano, 1988; Hoyos and Lascano, 1985).

Adding animal consumption to the total litter deposition gives a total DM

Table 1. Weight gain of Nelore cattle grazing pastures of *Brachiaria humidicola* alone or *B. humidicola/Desmodium ovalifolium* at three stocking rates, Itabela, BA, Brazil.

Pasture	Stocking rate (hd/ha)	Daily weight gain			
		1988-1989		1992-1993	
		g/hd	g/ha	g/hd	g/ha
B. humidicola	2	438	876	339	678
	3	430	1,289	287	862
	4	378	1,512	270	1,080
	Mean	415	1,226	299	873
B. humidicola/ D. ovalifolium	2	423	847	377	754
	3	489	1,468	377	1,070
	4	351	1,405	295	1,178
	Mean	421	1,240	343	1,001

SOURCES: Pereira, 1991; C. de P. Resende and J. M. Pereira, unpublished data.

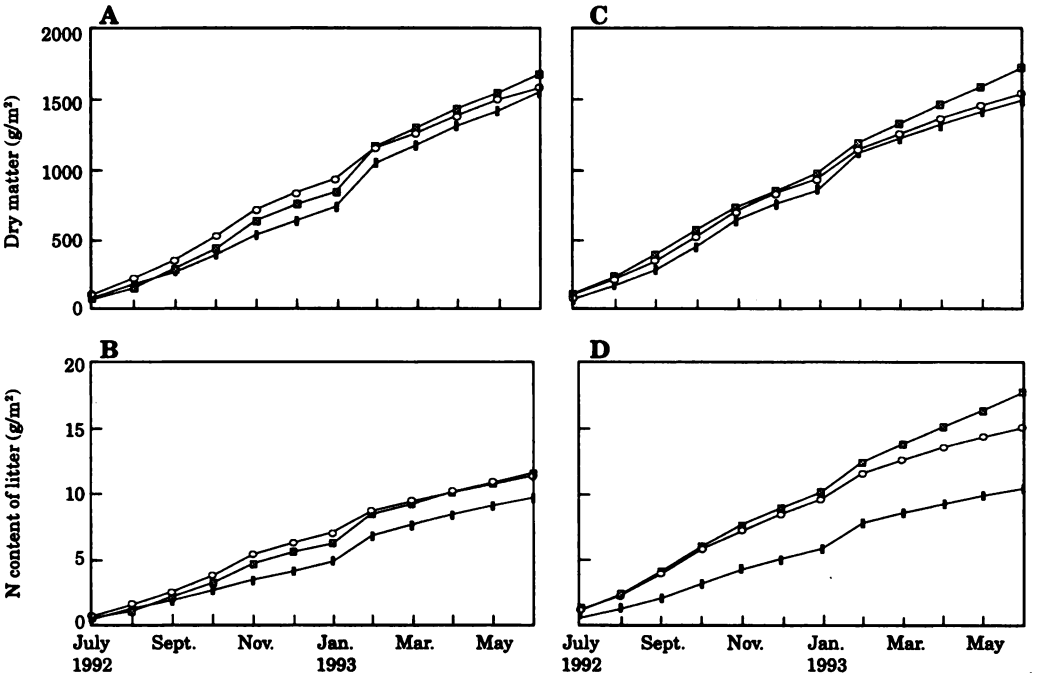

Figure 2. Total dry matter (DM) and N content of litter deposited in pure grass and grass-legume pastures at three stocking rates: ■ = 2 an./ha; ○ = 3 an./ha; and ▮ = 4 an./ha. (A) and (B) = *Brachiaria humidicola*; (C) and (D) = *B. humidicola/Desmodium ovalifolium*. (ESSUL/CEPLAC, Itabela, BA, Brazil, unpublished data; C. de P. Resende, J. M. Pereira, R. B. Cantarutti, M. Richter, B. J. R. Alves, G. Cadisch, and R. M. Boddey, unpublished data.)

production of 19-22 t/ha per year in either the pure *Brachiaria* or the grass-legume pasture, differing little with stocking rate (Table 2). However, the total N yield was considerably higher in the grass-legume pasture, especially at the two lower stocking rates, where the proportion of legume in the sward was still considerable (39% and 16%, for 2 and 3 hd/ha, respectively). At 3 hd/ha or fewer, *D. ovalifolium* persisted well in the sward, and other *B. humidicola* pastures at this experiment station have maintained a good proportion of this legume for more than 10 years under grazing (J. M. Pereira, 1994, personal communication).

A ^{15}N-isotope dilution experiment was conducted at the edge of the main paddocks to estimate the proportion of N derived from BNF in the *D. ovalifolium*. At the first harvest, 3 months after establishment, the proportion of N derived from BNF was only 30%, but 2 months later, this rose to 53%. In this satellite study, the legume was grown in rows, alternated with either one or two rows of *B. humidicola* to simulate a mixed sward, and soil fertility was similar to that of the paddocks in the main study. This proportion of BNF in the legume is low, compared with results of other studies on tropical forage legumes (Cadisch et al., 1994b; Vallis et al., 1977), but other studies suggest *D. ovalifolium* is not a very efficient N_2 fixer (Cadisch et al., 1989; Viera-Vargas et al., 1995), and this may have been aggravated by P or K deficiency.

Using the above data, a simple mass balance can be constructed for each pasture (stocking rate 3 hd/ha), based on that used by Cadisch et al. (1994b) (Figures 3A and 3B). Nitrogen losses

Table 2. Total dry matter (DM) and N production, animal consumption, and N contribution of biological N_2 fixation (BNF) in pastures of *Brachiaria humidicola* alone and *B. humidicola/Desmodium ovalifolium* at three stocking rates.

Pasture	Stocking rate (hd/ha)	Litter deposition		Total plant production[a]		Legume present[b] (%)	BNF contribution[c] (kg/ha)
		DM (t/ha)	N (kg/ha)	DM (t/ha)	N (kg/ha)		
B. humidicola	2	16.0	115	22.1	197	-	-
	3	15.7	114	22.8	196	-	-
	4	15.3	95	21.4	177	-	-
B. humidicola/ D. ovalifolium	2	17.0	177	21.5	267	39.0	73.5
	3	15.2	151	19.7	241	16.4	28.2
	4	14.7	103	19.2	193	1.6	2.7

a. Sum of total litter deposition and animal consumption (see text).

b. In material on offer.

c. Based on estimate from ^{15}N satellite experiment of 53% of N derived from BNF.

SOURCE: C. de P. Resende, J. M. Pereira, R. Cantarutti, M. Richter, B. J. R. Alves, G. Cadisch, and R. M. Boddey, unpublished data.

from the sward, apart from urine and dung patches, were assumed to be low and to be balanced by atmospheric and rainfall inputs. Cattle were also assumed to excrete N equally between dung and urine, so that losses from dung were 10%, and losses from urine 50%.

In the grass-legume sward, almost no net loss or gain of N occurred to soil OM (-5 kg/ha per year), and in the pure *Brachiaria* pasture, a small loss of N (-30 kg/ha per year) occurred. As the contribution of BNF associated with the *B. humidicola* has not been investigated, it was assumed to be negligible, but if a credible contribution of 30 kg/ha of N per year is assumed, then both pastures at this stocking rate experienced an overall neutral or slightly positive N balance. This shows the possible ecological importance of even so small a BNF contribution to the sustainability of this system.

Even after 5 years under this pasture, the soil showed no gain in total N. In view of spatial variability, there would have to be perhaps as much as a 10% change (900 kg/ha) in total N in the profile for it to be detected with certainty. This illustrates the utility of measuring fluxes of N in the cycle rather than pool sizes. Dynamic modeling, using computerized systems, such as Century (Parton et al., 1987) or Phoenix (McGill et al., 1981), should predict better the future productivity and sustainability of these pasture systems.

Factors Affecting Sustainability of *Brachiaria* Pastures

In both pure grass and grass-legume systems, a large amount of N is obviously being recycled back to the soil surface, about 70% of it in litter. In N-fertilized swards, especially in temperate regions, where litter production is much lower, more N is recycled via animal excretion than via litter; these losses, especially via urine, are critical, not only because of the loss to the production system but also, especially, because of the pollution of the atmosphere (NH_3 volatilization) and water reserves (NO_3^-).

For a moderately grazed *Brachiaria* pasture to maintain its productivity, the limiting factor will be the mineralization of organic N from litter residues; hence the importance of introducing a legume into the pasture to raise the quality of the

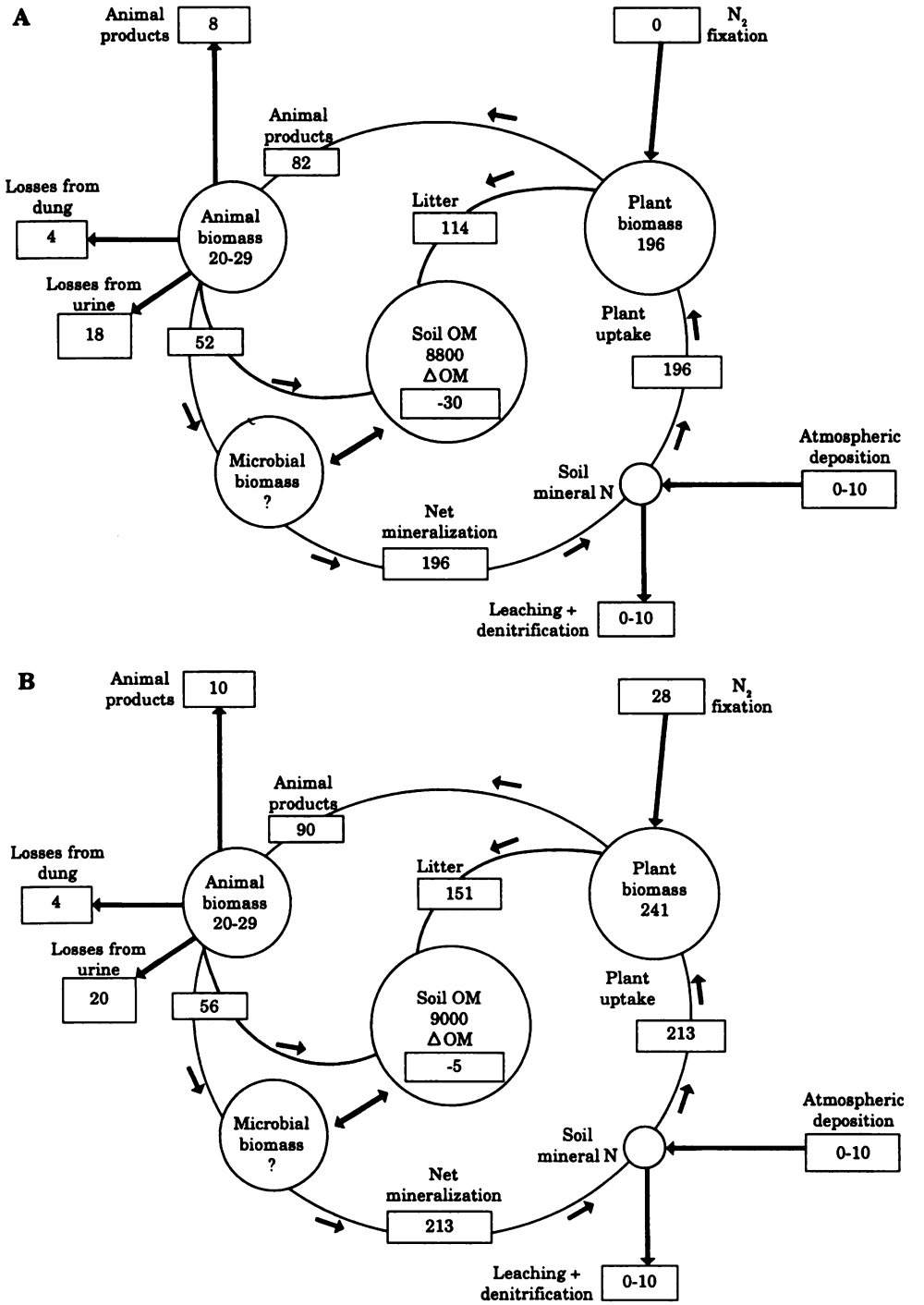

Figure 3. Nitrogen cycle in pastures of (A) *Brachiaria humidicola* and (B) *B. humidicola* / *Desmodium ovalifolium* at three stocking rates. Boxes represent fluxes; circles represent pool size; and numbers are values in kg/ha. Assumptions: (i) 90% of N in animal intake was deposited as animal excretion and equally distributed between feces and urine; and (ii) precipitation of N is equal to gaseous and leaching losses from pasture, except from animal excretion. (ESSUL/CEPLAC, Itabela, BA, Brazil, unpublished data; C. de P. Resende, J. M. Pereira, R. B. Cantarutti, M. Richter, B. J. R. Alves, G. Cadisch, and R. M. Boddey, unpublished data.)

animal diet and the degradability of the litter residues. Different tropical legumes have widely different rates of degradation (Thomas and Asakawa, 1993a). The problem is that a legume of high digestibility and N content, low in lignin and polyphenols and hence readily decomposable, may not persist under grazing in association with *Brachiaria* grasses, which are less palatable.

The problem of the persistence of tropical legumes in pastures of *Brachiaria* and other exotic grasses has been addressed by several authors (e.g., Marten et al., 1989; Peres, 1988; Thomas, 1995). Suitable legume species and genotypes must be selected for each edaphoclimatic region, and a great deal of research remains to be done in this area. The basic attributes required of the legume are that it should tolerate the acid soil and climatic conditions in the relevant region (drought, waterlogging, cool season); be compatible with the grass species used; and, where relevant, show good seed production, with seed that remains viable over the dry season so that the legume plant population can be reestablished at the onset of the rains. In all cases, however, the persistence of the legume will depend greatly on management. Tropical forage legumes usually require more P and Ca, and less K than *Brachiaria*; lime and phosphate fertilization would therefore favor their persistence.

As is apparent from the study in Bahia (Pereira et al., 1992a; 1992b), animal management is also critical. In this and other cases, high stocking rates or long rest periods in rotational grazing (J. M. Spain, G. Leite, L. Vilela, C. Gomide, and C. M. da Rocha, unpublished data) may cause the legume to decline. To select a suitably persistent legume and to pursue a suitable management strategy may seem a daunting task, but the potential benefits of sustainable and productive pastures over millions of hectares of underused, potentially degradable land in South America make the effort worthwhile.

Recent studies with *A. pintoi* or *A. repens* suggest that suitable genotypes of these legumes can be highly productive and persist well in *Brachiaria* pastures in many areas of the South American savannas, at least in those with no severe dry season (Pizarro and Rincón, 1994).

Environmental Impact of *Brachiaria* Pastures

Degraded pastures have an especially negative impact on the environment, on both a local and regional scale. If grass pastures are continuous, then the reserves of soil OM are not depleted as they are under continuous annual cropping with frequent plowing. In fact, OM levels may be higher under long-term *Brachiaria* pastures than under native savanna or even forest (Fisher et al., 1994; Veldkamp, 1993). However, the very high C-to-N ratio in this OM can prevent the release of mineral N for plant growth, and a large proportion of the soil may therefore remain unprotected by vegetation.

Well-maintained, productive pastures, in contrast, can have a decidedly positive environmental impact. As discussed earlier, the losses of nutrients from a productive pasture (unless fertilized with high rates of N fertilizer or manure) are unlikely to cause significant pollution of water resources. Similarly, atmospheric pollution by ammonia volatilized from urine patches is unlikely to be ecologically significant at prevailing levels of animal production.

No data are available on the changes in emissions of nitrous oxide (a potent contributor to the "greenhouse effect" and an agent in the destruction of the ozone layer) when improved pastures are established, but this gas is a byproduct of nitrification (thought to be very low in grass swards) and one of the products of denitrification, which occurs only when

high nitrate levels exist in badly drained soils (Minami et al., 1993).

Another gas responsible for the "greenhouse effect"—methane—is produced in large quantities, and this is related to the quality of the forage consumed. Both native and sown pastures in the process of decline produce forage of low digestibility and protein content, and animals grazing this forage emit large quantities of methane. Those grazing on a vigorously growing *Brachiaria* pasture, with high-quality forage, emit far less methane per unit of animal product (Minami et al., 1993).

One positive environmental impact of *Brachiaria* and *Andropogon* pastures in the savanna regions of South America is carbon sequestration. Large amounts of C are sequestered and accumulate in the soil as roots and root residues. In the Llanos of Colombia (Carimagua Research Station), root biomass production under grazing in improved pastures of (1) grass alone (*B. dictyoneura* cv. Llanero) and (2) grass-legume (*B. dictyoneura* cv. Llanero-*C. acutifolium*) was compared with that in native savanna for 3 years (I. M. Rao, unpublished data). In the pure grass pastures, root biomass averaged about 6.2 t/ha; in the grass-legume pasture, 3.9 t/ha; however, in native savanna, it was only 1.8 t/ha.

Fisher et al. (1994) found that carbon levels in the soil below 40 cm were far higher under *Brachiaria* or *A. gayanus* pastures, especially in the presence of a forage legume, than under native savanna. These authors suggested that as much as 100-507 million tons per year of C could be sequestered in about 40 million hectares of improved (mainly *Brachiaria*) pastures in South America, and that this could significantly reduce the global increase of atmospheric CO_2, hence reducing the risks of global warming.

In the humid tropics of Costa Rica, Veldkamp (1993) quantified the changes in soil organic C storage and the resulting release of CO_2 after the conversion of tropical rain forest to improved or native pastures on two contrasting soil types. The use of the ^{14}C pulse-labeling technique showed that root DM production of an improved pasture, such as *B. dictyoneura* cv. Llanero (12 t/ha per year), was about twice that of a native pasture, such as *Axonopus compressus* (6 t/ha per year). A simple soil organic C model was also used in this study to calculate the cumulative net release of CO_2. From pastures with unproductive grass species (*A. compressus*), CO_2 release ranged from 31.5 to 60.5 t/ha (depending on soil type) in the first 20 years after forest clearing. Again depending on soil type, these cumulative emissions could be reduced by about 60%, to 12.0-24.7 t/ha, if more productive *Brachiaria* cultivars (e.g., *B. dictyoneura* cv. Llanero) were to be introduced into the area.

Conclusions

In summary, a vigorously growing *Brachiaria* pasture can have a positive environmental impact, and, at the same time, give high yields of animal products. Whether this productivity can be sustained, however, depends on suitable soil fertility and animal management strategies. The introduction of a forage legume could carry distinct benefits for animal production and sustainability of the system.

Future Research Priorities

Interdisciplinary research should be undertaken in the following areas:

1. *Pasture degradation*. Causes of pasture decline need to be evaluated in contrasting edaphoclimatic regions to develop viable management practices that will reduce pasture degradation and reclaim degraded areas for sustainable animal production.

2. *Pasture reclamation*. Suitable forage legumes should be identified for short- and long-term pastures. We need to quantify long-term effects of existing pasture reclamation systems on pasture productivity and soil improvement.

3. *Environmental impact*. Research is needed to quantify the changes in gains and losses of greenhouse gases in *Brachiaria* pastures, compared with native pastures.

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To save space, the following acronyms are used in place of publishers' names:

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

CPAC = Centro de Pesquisa Agropecuária dos Cerrados

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Agricultural Science

NZSAP = New Zealand Society of Animal Production

RIEPT = Red Internacional de Evaluación de Pastos Tropicales

TGSA = Tropical Grasslands Society of Australia

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Chapter 6

Pests and Diseases of *Brachiaria* Species

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Abstract

The main insect pests and diseases associated with *Brachiaria* pastures are considered, with emphasis on spittlebugs, the most damaging pests in tropical America. Outbreaks of the polyphagous burrowing bugs of the genus *Scaptocoris*, both in Brazil and Colombia, are of concern. Other pests discussed include leafcutting ants; the mound-building termites, *Cornitermes cumulans* and *Syntermes* sp.; the lepidopterans, *Spodoptera frugiperda* and *Mocis latipes*; the rhodesgrass scale, *Antonina graminis*; and the chinch bug, *Blissus leucopterus*. Important fungal and viral diseases of *Brachiaria* species are outlined. Most of these occur in Africa, the center of diversity of *Brachiaria*, but lately some—particularly foliar blight caused by *Rhizoctonia solani*; ergot, caused by *Claviceps* species; and guineagrass mosaic virus—have acquired importance in tropical America, and could become devastating where vast areas are planted to a single cultivar. Chemical control is not feasible in perennial pastures, and pest- and disease-resistant cultivars of *Brachiaria* need to be developed as a low-cost alternative. Promising control measures and future research needs are discussed.

Introduction

The beef cattle industry in tropical America, with its extensive production systems, depends on forage grasses for meat production. Several species of the genus *Brachiaria* comprise the most important of these. Because of their excellent adaptation, particularly of *B. decumbens* and *B. humidicola*, to low-fertility acid soils, they have been widely adopted throughout Central and South America. Their introduction, mainly in the savannas, has increased the carrying capacity of pasture lands previously occupied by low-yielding native grasses.

Brachiaria pastures are subject to several insect and disease problems; however, because pastures are considered low-value crops and because they occupy vast areas, chemical control, widely used in high-value crops, is too costly and seldom used for pastures. Therefore, effective low-cost control measures that farmers can easily adopt, such as pest- and disease-resistant cultivars, need to be developed. Because endophytes can also play a role in broad-spectrum disease and pest resistance (Bacon and White, 1994), an understanding of their role in *Brachiaria* may prove to be of great value in breeding and germplasm evaluation.

This paper reviews the main pests and diseases of *Brachiaria* species and current and promising control measures, with special emphasis on the Americas. Regional pest and disease problems are referred to by other contributions in this volume (Argel and Keller-Grein, Ch. 14; Pizarro et al., Ch. 15; Stür et al., Ch. 17).

Insect Pests of *Brachiaria*

In tropical America, insect pests of *Brachiaria* are native species that have adapted well to the introduced forage. The extensive monocultures of *B. decumbens* cv. Basilisk in the savannas

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have favored the buildup of some pest populations; those of most concern have been recorded by several investigators (Bergmann et al., 1984; Calderón C. and Arango S., 1985; Calderón C. et al., 1982; Silveira Neto, 1976; Pizarro et al., Ch. 15, this volume). The most evident and damaging pests of *Brachiaria* in tropical America are the spittlebugs, which have received the most attention from researchers. Other pests include termites, leafcutting ants, burrowing bugs, armyworms, and striped grassworms (Figure 1). Although originally from Africa and also used in Asia and Australia, *Brachiaria* is not as important in these regions as it is in Central and South America. Therefore, the entomological problems related to *Brachiaria* pastures have been reported almost exclusively for tropical America.

Spittlebugs (Homoptera:Cercopidae)

Spittlebug damage can result in the complete loss of available forage. These pests range from southern USA to northern Argentina, and are known as "spittlebugs" or "froghoppers" in the USA, "salivazo" or "mión" in Colombia, "candelilla" in Venezuela, "mosca pinta" in Mexico, and "cigarrinhas" in Brazil. Each locality has its own specific complex of spittlebugs, differing according to genus, the most important being *Zulia*, *Deois*, *Aeneolamia*, and *Mahanarva*.

In regions where a well-defined dry season occurs, the nymphs are first seen at the beginning of the wet season. After hatching from diapausing eggs, they establish themselves at the base of the plant, where they suck the sap and surround themselves with a frothy, spittle-like mass. One to several nymphs may be found inside each spittle mass. Inside this moist habitat, they go through several instars, emerging as adults, which then live on the aerial portion of the plant.

The life cycle duration and the number of generations depend on the spittlebug species and on local climatic conditions. In some tropical humid areas, the spittlebugs may be found all year, whereas in drier regions, the infestation period lasts only as long as the local wet season. Although nymphal feeding may cause some damage, Byers and Wells (1966) observed that the major damage is caused by the adults. These authors suggested that the toxic saliva injected during adult feeding interferes with photosynthetic activity. As a result, the *Brachiaria* leaves first appear whitish; later, necrotic lesions spread longitudinally toward the leaf apex. Under severe spittlebug attack, the entire aboveground portion of the plant appears dry and dead. This does not usually kill the plants, except seedlings, and a regrowth is expected; however, the damage may significantly reduce dry matter (DM) production and forage quality (Valério and Nakano, 1988; 1989), lowering the stocking rates of damaged pastures at least temporarily.

Although this severe damage to the plants is obvious, data are still needed to assess the full-season impact on animal production. As Pottinger (1976) pointed out, crop losses from pests are relatively easy to estimate because of their direct effects on crop yield. But assessing pasture pest damage in terms of animal production is complex, costly, and difficult.

Probably no single method will effectively control spittlebugs; a more appropriate strategy is to integrate various control tactics and to diversify pasture species, thus restricting damage to small areas.

Chemical control. In *Brachiaria*, insecticides are used in high-value areas, such as seed production plots; however, because of their high cost, they are seldom used in pastures. Further, the farmer's interest in chemically controlling spittlebugs does not develop until the damage becomes obvious. But the full expression of, for instance, *Zulia entreriana* damage in *B. decumbens*, takes about 3 weeks, while the adult lives for only about 10 days (Valério and Nakano, 1992). Thus, proper timing of insecticide

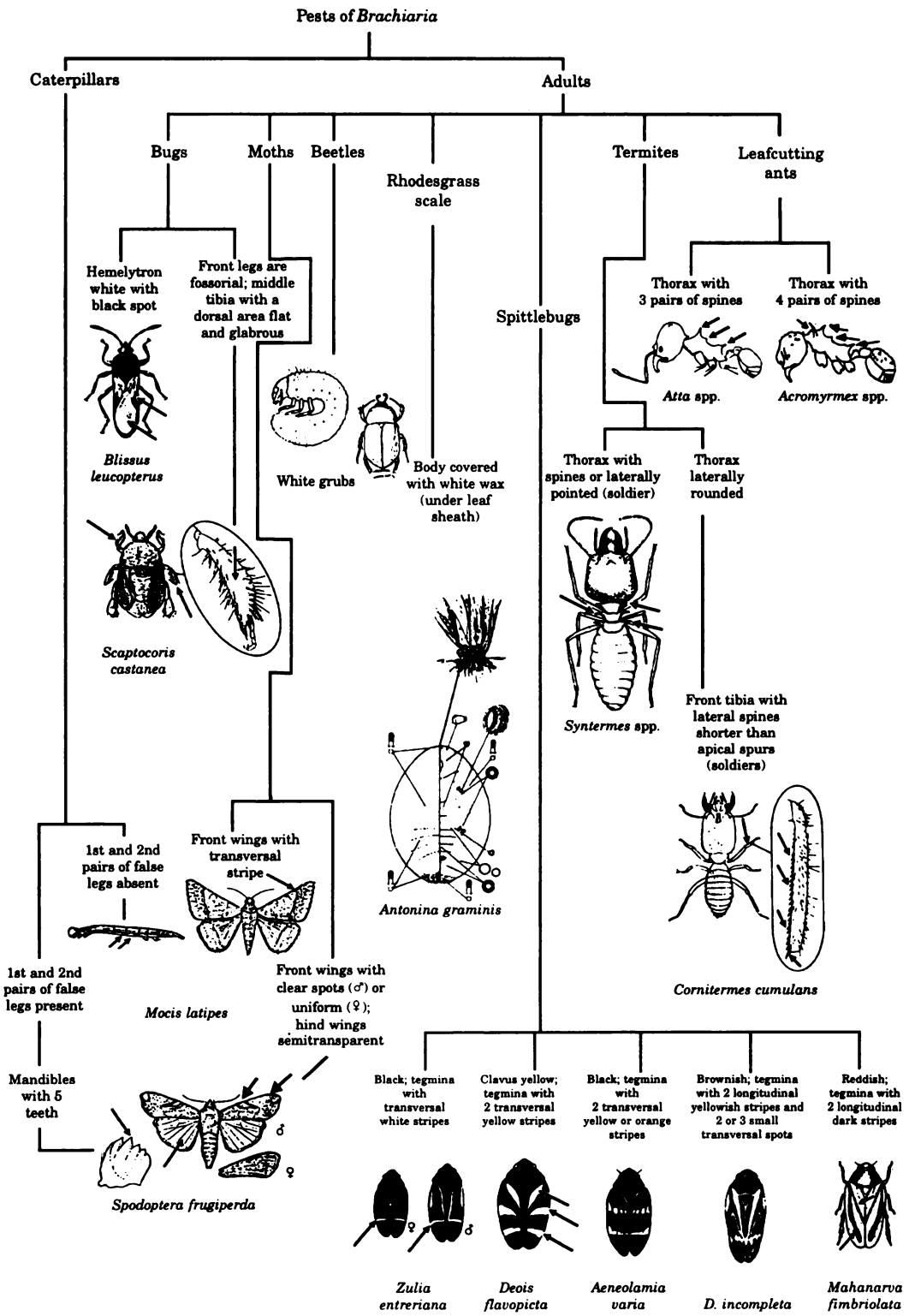

Figure 1. Some insect pests of *Brachiaria*. (Drawings are not to scale. Adapted from Zucchi et al., 1993.)

application is crucial to effective control, as most of the adult population, which is responsible for the damage, is already dead by the time damage becomes noticeable. Fertilizing the pasture to compensate for spittlebug damage may be more cost-effective than using insecticide, as Prestidge and East (1984) demonstrated for the grass grub, *Costelytra zealandica*, in New Zealand.

Biological control. Biological control of spittlebugs has been attempted to a limited extent (Barbosa, 1990; El-Kadi, 1977), but little research has been conducted to assess the real potential of this strategy. A major attempt at augmentative biological control, using the fungus *Metarrhizium anisopliae*, gave inconsistent results, and the method has fallen into disrepute. Nevertheless, biological control holds great potential, because *Brachiaria* pastures, being perennial, provide a fairly stable environment, which should favor the persistence of released natural enemies. Further studies are necessary on entomopathogenic fungi and other natural enemies. For instance, the hymenopteran, *Anagrus* sp., is an egg parasite (Pires et al., 1993); larvae of the fly, *Salpingogaster nigra*, are efficient predators of spittlebug nymphs (Marques, 1988; Páez et al., 1985); and adults of the fly, *Porasilus barbiellinii*, prey upon spittlebug adults (Bueno, 1987); and ants may influence spittlebug populations through predation of newly emerged nymphs (Hewitt and Nilakhe, 1986; Medina Uribe, 1993).

Cultural practices. Various studies have shown that populations of several insect species can be reduced by grazing management (East and Pottinger, 1983). The impact of grazing on insect numbers appears to be indirect, by affecting the microclimate and environmental conditions of the insect habitat (Martin, 1983). Besides being ecologically sound, the use of grazing animals to control pasture pests is also inexpensive, easily applied, and readily understood by farmers.

Attempts have been made to assess the effectiveness of such strategies: observations over a 3-year period by Valério and Koller (1993) showed that both nymph and adult spittlebug numbers decreased as grazing pressure increased. This finding supports earlier data (Koller and Valério, 1988) on the influence of litter accumulated at soil level on spittlebug populations: significantly lower numbers of spittlebug nymphs and adults were observed over 17 months in pastures where litter was removed. The amount of litter probably increases under low stocking rates. Hewitt (1986) also observed a higher spittlebug egg survival in *Brachiaria* pastures taller than 30 cm, which collected an abundance of litter. Other grazing management studies (Cosenza et al., 1989; Hewitt, 1988; Ramiro et al., 1984) generated contradictory recommendations for the use of grazing animals to control spittlebugs. This strongly suggests the need for further studies. Such a control strategy may be constrained by factors such as weather, topography, restricted application time, and possible detrimental effects of hard grazing and trampling on pasture production (East and Pottinger, 1983); however, this approach may play an important role in combination with other control measures.

Host-plant resistance. Host-plant resistance offers the advantage of being a low-cost method of controlling pasture pests, and one that farmers can easily adopt. Great effort has been devoted to finding grasses resistant to spittlebugs. At first, several grass species from various genera were evaluated (Botelho et al., 1980; Menezes and Ruiz, 1981), some of minor importance in terms of area planted; for example, *Setaria*, *Cynodon*, *Hyparrhenia*, *Digitaria*, and *Melinis*. Of the *Brachiaria* species included in those trials, *B. decumbens* cv. Basilisk and *B. ruziziensis* were rated susceptible, while *B. humidicola* was rated resistant. However, according to Painter's classification of mechanisms of resistance (Painter, 1951), *B. humidicola* is considered tolerant, as it suffers less

damage, within certain limits, than more susceptible species under the same insect pressure.

In the humid tropics of Brazil, the susceptible cv. Basilisk was largely replaced by the tolerant *B. humidicola*; however, despite this tolerance, or perhaps because of it, the spittlebug population in the region reached levels high enough to cause severe damage even in *B. humidicola*.

Cosenza et al. (1989) and Nilakhe (1987) reported a high level of spittlebug resistance in *B. brizantha* cv. Marandu. The mechanism of resistance here is antibiosis; that is, the grass has an adverse effect on the survival and development of spittlebugs. The basis of this resistance, however, is not yet fully understood. Although this cultivar has excellent resistance to spittlebugs, it requires more fertile soils than the widely planted *B. decumbens* cv. Basilisk, and has been adopted mostly, but not exclusively, in more fertile areas.

More recently, *B. dictyoneura* cv. Llanero[1] was released in Colombia as tolerant of spittlebug. Subsequent studies have shown, however, that this cultivar is an excellent host for spittlebug nymphs (Ferrufino and Lapointe, 1989), and high levels of damage to this grass have been observed in Colombia and Central America.

The introduction to South America of a large collection of new *Brachiaria* germplasm from Africa has stimulated the search for host-plant resistance to spittlebugs. Based on this germplasm, provided by CIAT, field data on spittlebug damage or infestation levels on accessions have been reported from Ecuador (Costales, 1992), Bolivia (Ferrufino, 1986), and Peru (Reátegui, 1990). A more efficient screening technique to identify resistance has been developed and used, mostly in the greenhouse (Ferrufino and Lapointe, 1989), but also under field conditions (Lapointe et al., 1989a). Equally important, mass-rearing procedures have been established (Lapointe et al., 1989b) for a continuous supply of spittlebug eggs, nymphs, and adults for screening trials.

Although several spittlebug species attack *Brachiaria* pastures, *Aeneolamia varia* in Colombia and *Zulia entreriana* in Brazil have been the focus of the most intensive studies (Lapointe et al., 1992; Valério, 1992). Antibiosis in various *Brachiaria* accessions is being measured by parameters such as nymphal survival, duration of nymphal period (Figure 2), and dry weight of females.

A large part of the germplasm collection maintained by CIAT has been screened, and sources of resistance identified (J. W. Miles, 1994, personal communication). In Colombia, Lapointe et al. (1992) reported 11 accessions from six species of *Brachiaria* as being at least as resistant as *B. brizantha* cv. Marandu. On two accessions of *B. jubata* (CIAT 16531 and CIAT 16203), molting was disrupted, and many nymphs and pharate adults died while still encased within the previous nymphal exuviae. The exact plant component responsible for this antibiotic effect has not yet been identified, but an insect growth regulator is indicated.

According to Lapointe et al. (1992), at least one other type of antibiotic resistance toward spittlebug exists. In the commercial cv. Marandu, a toxin or an antifeedant that deters feeding, leading to death by starvation and desiccation during nymphal stadia, may be involved. Additional studies are required to better understand the mechanisms of resistance.

The resistance of cv. Marandu is known to be stable and effective against several species and genera of spittlebugs. In Brazil, Valério (1992) selected eight other accessions (different from those selected at CIAT), all of *B. brizantha*, as resistant, based on nymphal survival and

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

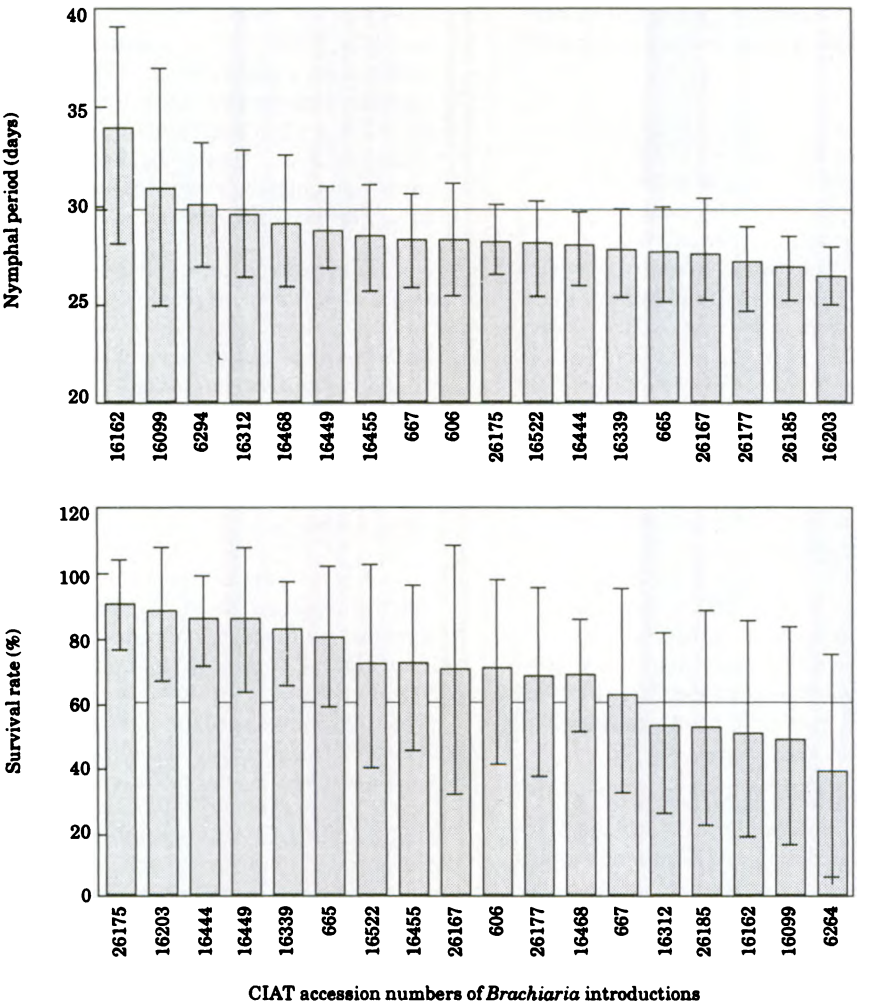

Figure 2. Nymphal period and survival rate of the spittlebug *Zulia entreriana* in some *Brachiaria* introductions.

duration of nymphal period of *Z. entreriana*. However, he obtained different results with an accession of *B. jubata* (CIAT 16203). High nymphal mortality of *A. varia* had been observed on this accession in Colombia, but *Z. entreriana* showed high nymphal survival rates and a short nymphal period on the same accession (J. R. Valério, unpublished data). This emphasizes the need to determine possible variability in response of resistant materials to different spittlebugs within the species complex in tropical America.

Screening for resistance is a continuing process; new sources of resistance have been identified and are available for inclusion in breeding programs. Escandón D. (1993) studied inheritance of reaction to spittlebug in progenies from interspecific crosses between *B. ruziziensis*, *B. brizantha* cv. Marandu, and *B. decumbens* cv. Basilisk. They showed a relatively high heritability of this character, suggesting a simple inheritance.

No other *Brachiaria* cultivar released in the last 10 years shows

spittlebug resistance comparable with that of *B. brizantha* cv. Marandu. After being widely adopted by farmers and often planted where soil fertility was too low to maintain satisfactory production, in Brazil, it is now being replaced again by the susceptible *B. decumbens* cv. Basilisk. Ramiro and Barbosa (1986) pointed out that despite the great research effort directed at spittlebug control over the years, not much has been provided to farmers in the form of practical and effective control measures. Diversifying pastures with resistant grasses holds great potential for containing the damage done by spittlebugs.

Burrowing stink bugs (Hemiptera:Cydnidae)

The burrowing bugs of the genus *Scaptocoris* feed on a variety of host plants (Becker, 1967), which ensures their survival over large areas. They occur in most tropical American countries, and their economic importance has been recognized for many years on crops such as cotton, sugarcane, rice, peanut, maize, tobacco, and beans, as well as on cultivated and wild grasses, in which they are predominantly found (Puzzi and Andrade, 1957).

Not much is known about their biology. Both nymphs and adults live in the soil, feeding on roots. The nymphs are whitish; the adults, usually about 10 mm long, are brownish, with front legs adapted for digging. The strong odor they emit when the soil is disturbed gives them their common name, stink bug. During wet periods, the insects remain in the upper soil layers, but in drier conditions, they move down to depths between 1.5 m (Puzzi and Andrade, 1957) and 4 m (Costa and Forti, 1993) in friable soils.

Recently, this pest has been reported as causing severe damage in pastures of different *Brachiaria* species in Colombia (A. Acosta and P. Hernández, 1992, personal communication), in Venezuela (Pizarro et al., Ch. 15, this volume), and in Brazil, where they killed thousands of hectares of pastures, mainly of *Brachiaria*, in the state of Mato Grosso alone (Correia et al., n.d.; Costa and Forti, 1993; Mendes et al., 1993; Ramiro et al., 1989). The species that attacked *Brachiaria* in the Colombian departments of Meta and Casanare was identified as *Cyrtomenus minor* Berg. (Hemiptera) (R. C. Froeschner, 1994, personal communication). Mendes et al. (1993) verified that the stink bugs occurred almost exclusively in sandy soils, in which they can probably move with ease.

Damage is caused by the insects sucking on the roots. Generally, significant losses have already occurred by the time infestations of *Scaptocoris* are detected. In small numbers, the bugs retard plant development, which may often go unnoticed; however, in large numbers, they kill the *Brachiaria* plants, altering pasture composition by allowing weed invasion.

Persistent organochlorine insecticides provided effective control, until they were withdrawn from use in agriculture. Others have been tested, but they are more expensive and less effective than the organochlorines. As Ramiro et al. (1989) pointed out, chemical control of *Scaptocoris* is feasible in annual crops, as it can be done once, during soil preparation, before planting. But in perennial pastures, which are also low-value crops, chemical control would be difficult and expensive. It requires repeated applications of a low-persistence insecticide, and depends on high soil moisture and rain to enhance its activity.

Thus, other control methods must be developed around the use of resistant plants and management practices, such as crop/pasture rotation, nowadays recommended for pasture renovation, to deal with serious and persistent attacks.

Leafcutting ants (Hymenoptera:Formicidae)

Leafcutting ants (tribe Attini) are a distinctive feature of the lowland savannas of Colombia and Venezuela and

the Cerrados of Brazil. Two species are particularly important: *Acromyrmex landolti*, whose host range within the Gramineae makes it a pest that impedes pasture development in the neotropical savannas (Robinson and Fowler, 1982), and *Atta laevigata*, which cuts both grasses and broadleaf vegetation. These ants affect both the botanical composition (Etter and Botero, 1990) and the soil physical characteristics of the savannas.

Colonies of *A. landolti* excavated as much as 1.5 m^3/ha of soil during 2 months of the dry season in eastern Colombia (Lapointe et al., 1990). This species is moderately polymorphic but has no soldier caste. It builds small (10,000 individuals) but numerous (up to 2,000/ha) nests in the open savanna. Each nest, with a single entrance (Lapointe et al., 1993), may have 3 to 10 chambers, extending down through the soil profile directly below the entrance. Colonization in susceptible swards may occur over several years, through founding queens or migration. Apparently, colonies of *A. landolti* do not remain at a given location for longer than 1 year, but move to new sites, although little is understood about this behavior.

Atta laevigata inhabits the open savanna in the Eastern Plains of Colombia. This species—as well as *A. cephalotes*—builds large colonies, covering several square meters, with numerous chambers that can reach a depth of 5 m and contain about a million individuals. Both species are markedly polymorphic and have a soldier caste as well.

Damage. *Acromyrmex landolti* damage in susceptible pasture grasses is usually most severe during establishment, particularly in highly infested areas of native savanna. During germination, damage appears in the form of cut seedlings and patchy establishment of the pasture. Highly infested swards of the susceptible *Andropogon gayanus* show not only loss of leaves but also pruning of roots by ants, whose colonies are characteristically located at the bases of the grass clumps.

Colony density. Surveys conducted in native savanna and introduced grasses in eastern Colombia demonstrated that the density of *A. landolti* colonies in the savanna is highly variable; there are areas of low density where it might be possible to successfully establish even susceptible cultivars. It was also determined that the distribution of colonies in infested savanna was highly aggregated, related to microtopography and surface runoff of rainwater.

A method was developed to estimate populations based on the distribution pattern, and a threshold was determined for establishment of the highly susceptible *A. gayanus* cv. Carimagua 1 (Serrano et al., 1993).

Host-plant resistance. Surveys suggested that cultivars of the genus *Brachiaria* were resistant to *A. landolti* (Lapointe et al., 1990). In native savanna, mean colony density was 567/ha (n = 136); at some sites, it was as high as 4,000 colonies/ha. In marked contrast, however, no colonies of *A. landolti* were found in pastures of *B. humidicola*, and almost none in pastures of *B. decumbens* and *B. brizantha*.

At the time, it was thought that resistance to leafcutting ants was a general attribute of *Brachiaria*; hence, that the ants were not a pest of this genus. Subsequent investigation, however, demonstrated that at least one commercial cultivar, *B. dictyoneura* cv. Llanero (CIAT 6133) was as susceptible to seedling damage by cutting as the susceptible control, *A. gayanus* cv. Carimagua 1 (CIAT 621). Numbers of established seedlings of cvs. Llanero or Carimagua 1 were less in nonprotected (infested) plots than in protected (noninfested) control plots. In contrast, numbers of seedlings did not differ between infested and noninfested plots of *B. decumbens* cv. Basilisk (CIAT 606), *B. humidicola* cv. Humidícola (CIAT 679), or *B. brizantha* cv. Marandu (CIAT 6294) (Lapointe, 1993). These cultivars were also resistant to leafcutter colonization over 3 years after establishment, while

the susceptible cvs. Llanero and Carimagua 1 were heavily colonized. Thus, while resistance to *A. landolti* appears to occur frequently, it cannot be considered a general characteristic of the genus *Brachiaria*, and care should be taken to guarantee inclusion of this valuable trait in new hybrids.

The mechanism of *Brachiaria* resistance to leafcutting ants (both *Acromyrmex* and *Atta*) consists of inhibiting the attine symbiotic fungus that comprises the principal food of the colony (Lapointe, 1993; S. L. Lapointe, unpublished data). Crude aqueous extracts inhibited growth of the symbiont on artificial media in the case of cvs. Basilisk, Humidícola, and Marandu, compared with media without extracts and media with extracts of the susceptible cvs. Llanero and Carimagua 1. It should be possible to identify the chemical components responsible for this inhibition and to develop a chemical screening method for rapid selection of *Brachiaria* hybrids.

Control. Common methods of controlling leafcutting ants are to inject insecticides directly into the nest entrance or use toxic baits formulated with persistent insecticides. Toxic baits based on an attractive matrix consisting of orange pulp have been widely used to control *Atta* species. However, the matrix is not attractive to *A. landolti*, perhaps because of the restricted host range of this species within the Gramineae. Soil preparation destroys colonies of *A. landolti* (Lapointe et al., 1990); however, this ant is able to recolonize rapidly in susceptible swards (Lapointe et al., 1993).

The high cost of chemical control (Lapointe, 1993) makes host-plant resistance the only feasible and stable control option in areas commonly infested with *A. landolti*. A method has been developed for estimating colony density in areas to be prepared for sowing; it takes into consideration the highly aggregated distribution of colonies in the savanna (Serrano et al., 1993). Estimates of colony density should be made before planting in areas where the use of a susceptible cultivar, such as cv. Llanero, is considered. Existing cultivars of *B. decumbens*, *B. humidicola*, and *B. brizantha* are highly resistant to leafcutting ants; planting these cultivars reduces or eliminates colonies from infested areas, which can then be rotated to susceptible crops, such as upland rice.

Termites (Isoptera:Termitidae)

Mound-building termites of the species *Cornitermes cumulans* are commonly seen infesting *Brachiaria* pastures, particularly in central Brazil and Paraguay. They are social insects, whose colonies live in strong earthen mounds about 1 m high.

The food habits of *C. cumulans* are still controversial: Cosenza and Carvalho (1974) found DM production was not reduced, even in highly infested areas, but Redford (1984) suggests that *C. cumulans* feeds on grass and herbaceous material.

In areas with annual crops, yearly tilling of the soil makes it difficult for the termites to establish colonies. However, more stable ecosystems, such as cultivated pastures—where the soil remains undisturbed for several years after pasture establishment and where food is abundant—favor the buildup of large termite populations. Siqueira and Kitayama (1983) observed that only 20% of the termite mounds counted in a natural undisturbed savanna were of *C. cumulans*, compared with 80% in cultivated pastures.

Termites are not regularly controlled in pastures; control measures are usually not attempted until high infestation levels reduce the grazing area and hamper the movement of machinery and even cattle in the pastures.

Control of *C. cumulans* is hard work. Insecticide is applied through a vertical opening made from the top of the mound into its core, and the treated mounds are manually or mechanically destroyed a few weeks later.

Another mound-building termite of concern in *Brachiaria* pastures is *Syntermes* sp. (possibly *S. molestus*), which constructs a soft, dome-shaped mound, 30-40 cm high, but often spread over several square meters. The termite is a potentially serious *Brachiaria* pest because it forages on living grass, particularly *B. humidicola* leaves. However, except in pastures of *B. humidicola*, high infestation levels of these termites have not been observed.

Lepidopterans (Lepidoptera:Noctuidae)

Larvae of the fall armyworm, *Spodoptera frugiperda*, and of the striped grassworm, *Mocis latipes*, are considered occasional pasture pests (Silveira Neto, 1976). Both have been known to occur throughout tropical America, and periodically infest *Brachiaria* pastures (Carvalho, 1976; Fuxa, 1989). The fall armyworm larva grows up to 4 cm long, being greenish when small and dark brown when full-grown, with a light midstripe along the back, ending in an inverted "Y" on the head. The full-grown larva of the striped grassworm is longer and more slender than that of the fall armyworm, and colored cream to brown, with large black spots that show when the body is fully extended.

Both species may occur simultaneously. The caterpillars chew the grass blades, causing damage in patches. When in large numbers, they may compete with cattle for food. The smaller larvae are often overlooked, but for successful control, treatment must begin at this stage. Besides low-toxicity chemical insecticides, the biological pesticide, *Bacillus thuringiensis*, can be used, particularly against *M. latipes*. On occasion, populations of these caterpillars have also been naturally controlled by a variety of parasitoids and predators.

Other insect pests

The chinch bug, *Blissus leucopterus* (Hemiptera:Lygaeidae), has been found in Brazil since 1975 (Reis et al., 1976). Although it is an important pest on crops such as maize and wheat, particularly in North America, the chinch bug in Brazil occurs on and damages chiefly *B. arrecta* (syn. *B. radicans*). The fact that even maize was not damaged when planted adjacent to highly infested and damaged areas of *B. arrecta* (Pereira and Silva, 1988) raises the question of whether this chinch bug was properly identified.

Another chinch bug species, *B. insularis*, was reported to cause severe damage in *B. mutica* in Venezuela (Carmona, 1983); however, no significant damage has been reported so far in the widespread commercial cultivars of *Brachiaria*.

The rhodesgrass scale, *Antonina graminis* (Homoptera:Pseudococcidae), has also been reported on *Brachiaria* pastures (Gabriel, 1983). Although a potentially important pasture pest, it has been successfully controlled by introducing the parasitoid *Neodusmetia sangwani* (Hymenoptera:Encyrtidae).

White grubs (Coleoptera: Scarabaeidae) constitute another minor pest of *Brachiaria* pastures (Calderón C. and Arango S., 1985). The stout, whitish body, with dark areas at the posterior end, lies in a typically C-shaped position. Living in the soil and feeding on the roots, white grubs can cause yellowish patches in *Brachiaria* pastures, which have sometimes been attributed to other causes.

Diseases of *Brachiaria*

Besides the insect pests described, *Brachiaria* species are subject also to several fungal and viral diseases that hamper their normal development. Most of the diseases reported occur in Africa (Lenné, 1990b), which is the center of diversity of *Brachiaria*, but in the last few years, some diseases have also acquired importance in tropical America, where the introduced *Brachiaria* species are extensively grown.

Fungal and bacterial diseases

Several fungal pathogens have been reported to attack *Brachiaria* species around the world (for a complete list see Lenné, 1990b).

In Colombia, foliar blight disease, caused by *Rhizoctonia solani*, is significant in some areas (Kelemu et al., 1995). A severe outbreak of foliar blight has recently been observed in large areas of pastures planted to *B. brizantha* cv. Marandu in the state of Acre in Brazil (C. D. Fernandes, unpublished data). The pathogen can inflict substantial foliar damage on susceptible genotypes of an extremely wide range of plant species (Baker, 1970), including *Brachiaria* and various tropical and subtropical crops (Galindo et al., 1983; Yang et al., 1990).

The fungus can survive for a long time in the soil or in infected plant debris as sclerotia, which are first seen as white masses on infected tissues. As these sclerotia mature, they become brown and loosely attached (Figure 3A), and fall to the soil, forming the primary source of inoculum for the next plant infections. Symptoms include initial water-soaked spots, followed by lesions of bleached centers with irregular brown borders (Figure 3B). The entire leaf blade could be blighted as the disease progresses and lesions coalesce.

Control of foliar blight through cultural practices, such as crop rotation and destruction of infected plant debris is not practical for perennial pastures such as *Brachiaria* grasses. The use of resistant genotypes is the cheapest method of disease control. We have recently developed reliable methods of inoculations and screening for identification of sources of resistance (Kelemu et al., 1995). Accessions of *Brachiaria* differ in their reactions to *Rhizoctonia* foliar blight—apparently resistance to foliar blight correlates with plant morphology and texture.

Rust, caused by the fungi *Puccinia levis* var. *panici-sanguinalis* and *Uromyces setariae-italicae*, is important in some parts of South America, particularly on accessions of *B. humidicola* (Fernandes et al., 1991; Fernandes and Fernandes, 1992; Fernandes et al., 1993; Lenné, 1990a). *Brachiaria humidicola* accessions differed in rust susceptibility in the Colombian Llanos (G. Keller-Grein, 1994, personal communication), and in the Colombian departments of Caquetá and Cauca (B. L. Maass, 1994, personal communication). At all three sites, cv. Humidícola (CIAT 679) was rated as the most susceptible.

Honeydew disease, or ergot, caused by *Claviceps* species, has been reported on *Brachiaria* in Africa—Ethiopia, Kenya, Malawi, and Zimbabwe—Australia, and

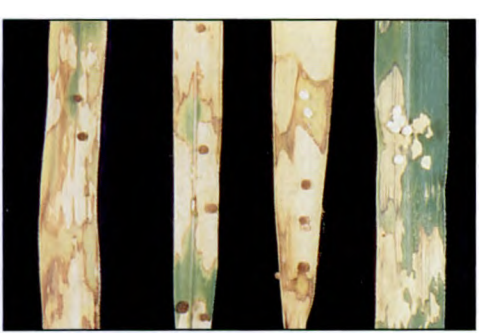

Figure 3A. Sclerotia of *Rhizoctonia solani* on *Brachiaria brizantha* cv. Marandu leaves.

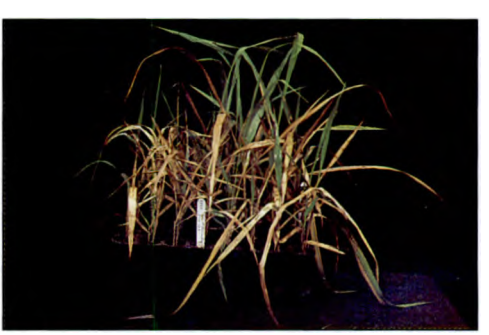

Figure 3B. Foliar blight symptoms caused by *Rhizoctonia solani* on *Brachiaria brizantha* cv. Marandu.

Figure 4. Honeydew symptoms on florets of *Brachiaria brizantha*.

India (Lenné, 1990b). In South America, this fungus has been reported in Brazil (Fernandes et al., 1992) and in Colombia (S. Kelemu, unpublished data) (Figure 4). Mature sclerotia of *Claviceps* spp. are known to produce toxic alkaloids, which, if consumed in large quantities, can cause serious injury or mortality in cattle and humans. Whether this disease in *Brachiaria* causes toxicity in cattle grazing on infected plants is not yet known. The sclerotial stage has not been observed in Colombia.

Another disease occasionally found in the field is bacterial blight, caused by *Xanthomonas* species, observed in Colombia in 1992 (S. Kelemu, unpublished data). Although it has not yet been demonstrated to be of economic significance, it could be of quarantine importance.

Viral diseases

Viral pathogens that affect *Brachiaria* species include several members of the sugarcane mosaic virus subgroup of potyviruses—sugarcane mosaic virus (SCMV), guineagrass mosaic virus (GGMV), maize dwarf mosaic virus (MDMV), and johnsongrass mosaic virus (JGMV) (Shukla et al., 1992)—as well as the digitaria striate rhabdovirus (DSV) and the maize streak virus (MSV). Their economic significance in *Brachiaria* pastures is not fully determined, but all plant viruses are of quarantine concern.

Potyviruses typically cause mosaic patterns on the leaves, leading to early senescence. Most are transmitted by aphid vectors, which acquire and transmit the virus in seconds; some may also be seedborne (Shepherd and Holdeman, 1965). Chemical control of the aphid vectors is not effective because of the mode of transmission, but breeding programs may lead to the development of virus-resistant cultivars of *Brachiaria*.

Guineagrass mosaic virus. Guineagrass mosaic virus strains were originally described in Côte d'Ivoire, in West Africa (Kukla et al., 1984; Lamy et al., 1979; Thouvenel et al., 1976; 1978). In Colombia and Brazil, a virus related to GGMV was first isolated from naturally infected *B. brizantha* (Morales et al., 1994). Recent work conducted at CIAT suggests that this virus is related to johnsongrass mosaic virus (F. J. Morales, unpublished data).

The natural host range of the *Brachiaria* potyvirus includes *B. decumbens* and *B. ruziziensis*. *Brachiaria dictyoneura* cv. Llanero, *B. humidicola*, and *B. jubata* may be infected under natural conditions, but symptoms are more apparent after artificial inoculation of young seedlings.

Systemically infected plants show characteristic rhomboid or eye-shaped lesions on affected leaves. As the disease progresses, various mosaic patterns and chlorotic patches develop, causing early leaf senescence. As long as infected plants are maintained under favorable agronomic conditions, the disease does not cause significant damage. However, its long-term effects on persistence or seed production of the grass are not known.

Maize dwarf mosaic virus. Maize dwarf mosaic virus is mainly prevalent in the USA, Africa, and Australia (Brunt et al., 1990). Its primary hosts are sorghum,

johnsongrass, and maize, but it also affects several other Gramineae if artificially inoculated (Ford et al., 1989). *Brachiaria platyphylla* is cited as an experimental host (Tosic and Ford, 1972). Strain A of MDMV has been reported to infect *B. eruciformis* in the USA (Rosenkranz, 1978). An unconfirmed report of MDMV affecting *B. reptans* in India is also found in the literature (Mali, 1985).

The most conspicuous symptoms induced by MDMV in susceptible hosts are mosaic and stunting. Like most other potyviruses, MDMV is transmitted by aphids. It may also be seedborne; therefore, seed lots should be carefully examined to prevent the inadvertent introduction of MDMV into virus-free areas.

Sugarcane mosaic virus. Sugarcane mosaic virus is distributed worldwide, hence *Brachiaria* plantings often come in contact with it. Following the revision of the SCMV subgroup of potyviruses (Shukla et al., 1992), strain B of MDMV is now considered a strain of SCMV. This strain was reported to infect *B. subquadripara* in Australia (Teakle and Grylls, 1973) and *B. eruciformis* in the USA. Its distribution in Central and South America is not known.

The main symptom induced by SCMV in *Brachiaria* is mosaic in different variegated patterns, depending on the age of the plant and time of inoculation. Besides being transmitted by aphid vectors, SCMV may spread through infected seed, by vegetative propagules, and by mechanical means (Brunt et al., 1990).

Johnsongrass mosaic virus. Johnsongrass mosaic virus is reported in the USA and in Australia (Brunt et al., 1990), its main hosts being sorghum and maize. It is a natural pathogen of *B. praetervisa* (Shukla and Teakle, 1989). Besides mosaic, the main symptom that JGMV induces in Gramineae is ring spots. Sensitive hosts may also suffer stunting.

Digitaria striate rhabdovirus. *Brachiaria subquadripara* (syn. *B. miliiformis*) is cited as a natural host of DSV. The virus was first observed in *Digitaria decumbens* (now *D. eriantha*) and *D. ciliaris* in the coastal areas of Queensland, Australia (Brunt et al., 1990). Its host range includes other Gramineae, such as oats, barley, and *Lolium multiflorum*. Symptoms include chlorotic striations and stripes.

The virus is transmitted in nature by the planthopper *Sogatella kalophon*, but not by seed or mechanical means. Vector specificity and host preference should limit the spread of DSV. Nevertheless, should it become a problem in *Brachiaria*, genetic control strategies should be possible, given its relatively limited host range. Chemical control of the virus is possible, but not practical, in perennial pastures.

Maize streak virus. Maize streak virus has been reported as a pathogen of *B. reptans* and *B. villosa* (syn. *B. distichophylla*) in Africa and India (IITA, 1994). Its natural host range includes several graminaceous plants such as sorghum and guineagrass (Brunt et al., 1990).

This geminivirus is transmitted by insect vectors belonging to the Cicadellidae (mainly *Cicadulina* species) in a persistent manner, but not through seed or by mechanical means.

Symptoms on maize and *Brachiaria* consist of chlorotic streaking and various other foliar lesions. Control of this virus would be extremely difficult, given its wide host range and severity, and the persistence of pastures. Chemical control of the leafhopper vector is only justified for special purposes, such as germplasm evaluation or seed multiplication. Genetic improvement is another possible control measure, and *Brachiaria* germplasm should be searched for sources of resistance to this virus.

Conclusions

To optimize the productivity, quality, and persistence of *Brachiaria* pastures, some insect and disease problems must be reduced. Host-plant resistance offers an economically sound and environmentally acceptable alternative to chemical control, which is not feasible in extensive production systems. Reasonable variability exists in the available *Brachiaria* germplasm, and sources of resistance to spittlebugs—a key pest of *Brachiaria* in tropical America—have already been identified. Methods for evaluating resistance, however, still need to be improved, especially selection methods for rapid screening of increasing numbers of progenies. Studies of the chemical and physical factors mediating the relationship between *Brachiaria* plants and spittlebugs, particularly the mechanisms of resistance, are also necessary. These may also lead to more efficient screening techniques that select directly for the desired characteristic.

The role of endophytic fungi in *Brachiaria* is as yet unknown, and should be studied. Endophytes can play a role in drought tolerance, competitiveness and persistence, nematode resistance, and broad-spectrum disease and pest resistance (Bacon and White, 1994). An understanding of their role in *Brachiaria* and other tropical grasses may prove to be of great value in breeding and germplasm evaluation.

An integrated and well-coordinated team effort, focused on the screening process, is required to accelerate the release of new pest- and disease-resistant *Brachiaria* cultivars.

References

To save space, the following acronyms are used in place of publishers' names:

AAB = Association of Applied Biologists

INIAA = Instituto Nacional de Investigación Agraria y Agroindustrial

IVITA = Instituto Veterinario de Investigaciones Tropicales y de Altura

SEB = Sociedade Entomológica do Brasil

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Chapter 7

Nutritional Quality and Animal Production of *Brachiaria* Pastures

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Abstract

Brachiaria grasses, especially *B. decumbens* cv. Basilisk (signalgrass), are the most widely grown pastures in subhumid and humid tropics. When fertilized with nitrogen and well managed, these pastures have high forage quality (measured as digestibility). Animal production is therefore high and relatively stable over time. Sometimes, however, animals fed on signalgrass and other *Brachiaria* species sicken, or show hepatogenous photosensitization, possibly caused by plant metabolites (steroidal saponins). Nitrate toxicity has been reported with *B. arrecta* and may occur with other species.

Although digestibility is high, it varies considerably among and within *Brachiaria* species, but is relatively stable across environments for any given material. The variation is caused mostly by different levels of crude protein (CP), possibly associated with inhibition of nitrification. Animal performance therefore differs from one *Brachiaria* grass to another. On acid, infertile soils, such as those of the Colombian Llanos, the protein content of *Brachiaria* grasses tends to decrease, thus reducing animal performance. But if *Brachiaria* grasses are grown in association with compatible legumes (e.g., *Arachis pintoi*) the performance of both animals and pasture can significantly improve.

Breeders should also take advantage of the variation in *Brachiaria* to select materials of higher quality than currently used commercial cultivars, and when breeding for spittlebug resistance.

Introduction

The genus *Brachiaria* includes both annual and perennial species. Of the perennial species, *B. brizantha*, *B. decumbens*, *B. dictyoneura*[1], *B. humidicola*, *B. mutica*, and *B. ruziziensis* are important as pasture plants in the subhumid and humid tropics. Review papers on *Brachiaria* species have either been restricted to *B. decumbens* in Australia (Loch, 1977) or have dealt mainly with origin, agronomy, and mineral nutrition of some *Brachiaria* species (Malavolta and Paulino, 1991; Paulino et al., 1987; Thomas and Grof, 1986) and, to a lesser extent, with forage quality and animal production (Gomide and Queiroz, 1994; Leite and Euclides, 1994; Vieira and Vieira, 1991).

In this chapter we review information on the nutritional quality of *Brachiaria* species and on animal production. We also discuss toxicity problems with *Brachiaria* species and possibilities for improving the quality of some commercial cultivars.

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1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Animal Production with *Brachiaria decumbens* cv. Basilisk

Of the *Brachiaria* species used in cultivated pastures, *Brachiaria decumbens* cv. Basilisk (signalgrass) is the most widely planted. Consequently, the quality of signalgrass has been measured in many cutting experiments and feeding trials, together with other well-known grass species. As results summarized in Table 1 show, the in vitro (IVDMD) and in vivo (DDM) digestibility of immature (leaf) and mature (whole plant) signalgrass is as high as or higher than that of other tropical grasses, such as *Panicum maximum*. Values of IVDMD in signalgrass have ranged from 60% to 70% in immature forage, and from 50% to 60% in mature forage—higher than the average (55%) for tropical forage grasses found by Minson (1990) from a review of the world literature.

Results from experiments designed to measure liveweight gain (LWG) of steers grazing signalgrass under different types of management are summarized in Table 2. In the humid environment of South Johnstone, Australia, Harding and Grof (1978) showed the high LWG potential of signalgrass with or without N fertilization. At similar stocking rates, LWG/ha per year on unfertilized signalgrass was 50% higher than that recorded earlier at the same location with unfertilized common *P. maximum* (Grof

Table 1. In vitro (IVDMD) and in vivo (DDM) digestibility of immature (I) or mature (M) *Brachiaria decumbens* cv. Basilisk and of other tropical grasses.

Species	IVDMD		DDM		Type of forage	Reference
	I (%)	M (%)	I (%)	M (%)		
B. decumbens	73	55			Whole plant from cuttings every 3 (I) and 12 (M) weeks (Kampala, Uganda)	Reid et al., 1973
Digitaria decumbens[a]	78	56				
Andropogon gayanus	66	51				
Hyparrhenia rufa	63	49				
Panicum maximum cv. Likoni	72	40				
B. decumbens	71	59			Whole plant from cuttings every 4 (I) and 13 (M) weeks (Mayaguez, Puerto Rico)	Coward-Lord et al., 1974
D. decumbens[a]	69	64				
H. rufa	76	53				
P. maximum cv. Guinea	61	46				
B. decumbens	60	53			Leaf tissue from cuttings every 3 (I) and 15 (M) weeks (Quilichao, Colombia)	Abaunza et al., 1991
A. gayanus	57	39				
H. rufa	48	39				
P. maximum cv. Guinea	59	37				
Paspalum plicatulum	54	29				
B. decumbens	67				Leaf from cuttings every 6 weeks (Guápiles, Costa Rica)	Vallejos A., 1988
P. maximum cv. Guinea	60					
B. decumbens	64	55			Whole plant from cuttings every 2 (I) and 8 (M) weeks (Selangor, Malaysia)	Wan Hassan et al., 1990
Setaria sphacelata	66	54				
Pennisetum purpureum	65	50				
P. maximum cv. Guinea	65	52				
B. decumbens			74	62	Plants from cuttings between 4 (I) and 12 (M) weeks and fed to buffaloes (Thailand)	Wanapat and Topark-Ngarm, 1985
P. maximum cv. Guinea			70	59		
B. decumbens			64		Plants of 6 weeks' regrowth fed to sheep (SE Queensland, Australia)	Norton et al., 1991
P. maximum cv. Guinea			56			
P. maximum cv. Petrie			59			
S. sphacelata			67			

a. Now *D. eriantha*.

Table 2. Liveweight gain (LWG) of steers grazing *Brachiaria decumbens* cv. Basilisk and other tropical grasses.

Location	Species	Stocking rate (hd/ha)	Annual LWG (kg/ha)	Average based on years	Reference
Australia,					
South Johnstone	*B. decumbens*				
	- N	3.5	573	4	Harding and Grof, 1978
	+ N (196 kg/ha)	3.5	717		
	+ N (196 kg/ha)	4.6	950		
	Panicum maximum (common)				
	- N	3.2	387	2	Grof and Harding, 1970
	+ N (168 kg/ha)	3.2	660		
Cape York Peninsula	*B. decumbens* + P	0.7	218	First year	Winter et al., 1977
		2.2	454		
	P. maximum + P	0.7	211	First year	
		2.2	300		
Southeast Queensland	*B. decumbens*				
	- N	3.0	438	3	Whiteman et al., 1985
	+ N (300 kg/ha)	5.0	602		
	P. maximum cv. Hamil				
	- N	3.0	477	3	
	+ N (300 kg/ha)	5.0 .	533		
	Paspalum plicatulum				
	- N	3.0	295	3	
	+ N (300 kg/ha)	5.0	273		
Colombia,					
Carimagua	*B. decumbens* + P	1.8	225	9	Lascano and Estrada, 1989
Brazil,					
Campo Grande, MS	*B. decumbens*	2.5	343	3	Euclides et al., 1993a
	P. maximum (common)	2.1	324		
	P. maximum cv. Tanzânia-1	2.3	446	3	Euclides et al., 1993b
	P. maximum cv. Tobiatã	2.5	414		

and Harding, 1970), whereas on fertilized signalgrass LWG was almost 1 t/ha (Harding and Grof, 1978). In a drier environment (Cape York Peninsula, Australia), signalgrass in association with legumes produced more LWG in heavily stocked pastures than a common *P. maximum* association (Winter et al., 1977). In southeastern Queensland, Australia, signalgrass fertilized with N and the improved *P. maximum* cv. Hamil produced similar LWG at both medium and high stocking rates (Whiteman et al., 1985) (Table 2). In Campo Grande, Brazil, animal gains on unfertilized signalgrass were 20% to 30% lower than on improved *P. maximum* cultivars (Tanzânia-1 and Tobiatã) (Euclides et al., 1993a; 1993b).

Reports of long-term grazing experiments are rare. One such experiment is being conducted in an Oxisol in the Colombian Llanos. A pasture of signalgrass fertilized every 2 years (10 P, 13 K, 10 Mg, and 16 S kg/ha) has been under continuous grazing for 16 years (1979 to 1994), with seasonal adjustment of stocking rate (1 head/ha in the dry season and 2 hd/ha in the wet season) (Figure 1). During the first 9 years, the annual average LWG was 125 kg/hd and 225 kg/ha, with minimum values of 48 kg/hd and 86 kg/ha in 1986 and maximum of 182 kg/hd and 328 kg/ha in 1981 (Lascano and Estrada, 1989). The low LWG in 1986 coincided with a season of unusually heavy rains (over 3,000 mm) and a severe spittlebug attack on the grass. Maximum LWG was recorded in a year with abnormal dry season rainfall (300 mm).

An analysis of the 16-year LWG data shown in Figure 1 indicates that this pasture does not show signs of degradation, despite periodic spittlebug attacks. The annual LWG recorded in 1994 (140 kg/hd) is similar to that recorded in the first year after establishment. However, this should not be interpreted to mean that spittlebug is not a problem in *B. decumbens*. Results shown in Figure 1 clearly indicate the large losses in LWG caused in a given year by spittlebug. Nevertheless, signalgrass has been persistent in this long-term grazing experiment, probably because of careful management, that is, seasonal stocking rate adjustment and maintenance fertilizer, which is not practiced for most commercial pastures.

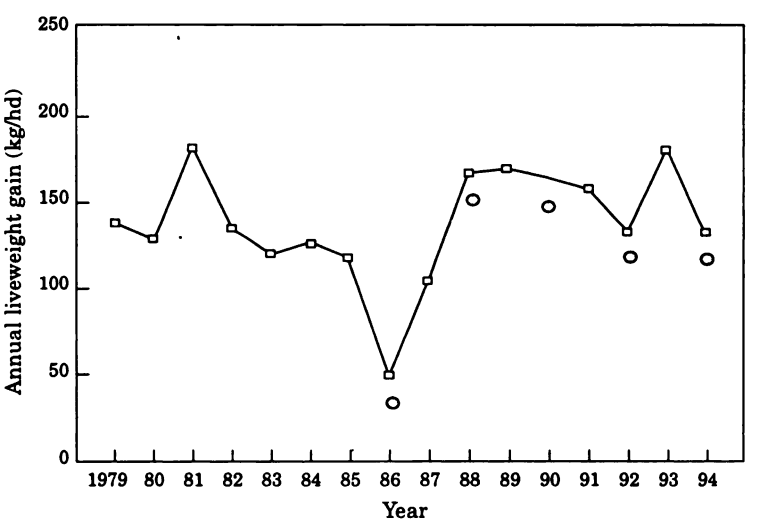

Figure 1. Annual average liveweight gain per head of livestock on pastures of *Brachiaria decumbens* cv. Basilisk in the Colombian Llanos, 1979-1994. (O = spittlebug attack.) (C. E. Lascano, unpublished data.)

Poor management (i.e., overgrazing and lack of fertilization) and spittlebug infestation are thought to be responsible for the degradation and consequent low animal production of large areas of signalgrass in the Brazilian Cerrados (Júnior et al., 1994; Válerio et al., Ch. 6, this volume; J. R. Valério, personal communication). Results from Mato Grosso do Sul, Brazil, showed that LWG on signalgrass could be doubled (from 120 to 250 kg/ha per year) with P fertilization (44 kg/ha) (Schunke et al., 1991). On less fertile soils in the Cerrados, LWG on signalgrass increased only by 60 kg/ha per year when the amount of P applied to the pasture was doubled (29 to 58 kg/ha) (V. P. B. Euclides, unpublished data). Under these conditions, animal performance was probably limited by low N levels in the soil (M. C. M. Macedo, 1994, personal communication).

In general, studies on digestibility and animal production show that cv. Basilisk is a good quality forage, and animal production with this cultivar is at least as high as with common *P. maximum*. This positive attribute of signalgrass, together with fast establishment and good seed yield, could explain its popularity among graziers, and should be kept in mind for programs designed to develop new *Brachiaria* cultivars.

Animal Production with Other Commercial *Brachiaria* Species

Forage quality

Susceptibility of *B. decumbens* cv. Basilisk to spittlebug has prompted pasture agronomists to evaluate other *Brachiaria* accessions and species. Average CP and IVDMD in leaf tissue of different *Brachiaria* accessions grown at sites with contrasting soils are summarized in Table 3. Except for *B. humidicola* grown in the Colombian

Table 3. Average crude protein (CP) and in vitro digestibility (IVDMD) of different *Brachiaria* species.

Species	Acc. (no.)	Leaves[a]		Type of forage	Reference
		CP (%)	IVDMD (%)		
B. brizantha	52	13 (10-16)	66 (56-75)	Leaves from plants in replicated single rows harvested every 6 weeks on an Inceptisol (Guápiles, Costa Rica)	Vallejos A., 1988
B. decumbens	26	14 (9-20)	71 (59-82)		
B. humidicola	21	13 (9-17)	68 (54-75)		
B. ruziziensis	8	14 (10-20)	71 (67-75)		
B. brizantha	150	-	60 (46-68)	Last expanded leaf from plants grown in unreplicated small plots on an Ultisol (Quilichao, Colombia)	M. J. Fisher, unpublished data
B. decumbens	32	-	66 (59-70)		
B. ruziziensis	14	-	64 (55-69)		
B. brizantha	260	-	65 (51-70)	Leaves from replicated single plants harvested every 6 weeks on an Ultisol (CIAT-Quilichao, Colombia)	J. W. Miles and C. E. Lascano, unpublished data
B. decumbens	44	-	65 (61-69)		
B. ruziziensis (tetraploids)	12	-	67 (64-72)		
B. humidicola	55	6 (5-8)	65 (60-70)	Leaves from plants in replicated small plots and harvested every 6 weeks during the rainy season on an Oxisol (Carimagua, Colombia)	G. Keller-Grein and C. E. Lascano, unpublished data

a. Numbers in parentheses are ranges.

Llanos, CP levels are high and within the range expected for immature leaves. Digestibility is also high, but with some differences among species. The IVDMD of *B. brizantha* was 2-6 units lower than that of *B. decumbens* and *B. ruziziensis*. A similar finding was reported by Valle et al. (1988) with *Brachiaria* species grown in the greenhouse. Even though small, these differences in digestibility need to be taken into account in ongoing breeding schemes designed to introduce spittlebug resistance into *B. decumbens*. In these programs, a tetraploid *B. ruziziensis* is used as a source of sexuality, and *B. brizantha* cv. Marandu as a source of spittlebug resistance (Miles and Valle, Ch. 11, this volume).

Voluntary intake of *Brachiaria* species has been measured in some studies. For example, in Jamaica, Grieve and Osbourn (1965) found high intakes (daily average of 80 g DM/kg $LW^{0.75}$) by sheep fed young (4-5 weeks), green regrowth of *B. decumbens* and *B. ruziziensis*. In Lavras, Brazil, however, the daily intake by sheep of the same *Brachiaria* species was considerably lower (50 g DM/kg $LW^{0.75}$) when the grass was fed as hay from forage harvested every 6 weeks (Rosa et al., 1983).

Similar results were recorded in Campo Grande, Brazil, where daily intake of signalgrass by steers was 45 or 70 g DM/kg $LW^{0.75}$ for mature or immature forage, respectively (O'Donovan et al., 1982). In contrast, voluntary intake of young (4 weeks) regrowth of *B. dictyoneura* and *B. humidicola* by confined sheep was low (60 g DM/kg $LW^{0.75}$ per day), even at high levels of forage allowance (C. E. Lascano, unpublished data).

Intake by steers grazing pastures of *B. humidicola* during the rainy season in the Colombian Llanos was also very low (1.3% of bodyweight) (Lascano et al., 1982). The poor animal performance (Tergas et al., 1982) was explained by a severe protein deficiency in the grass (4% CP in ingested forage) (Lascano et al., 1982).

Brachiaria species fall into two distinct quality groups: (1) a high-quality group that includes *B. brizantha*, *B. decumbens*, *B. ruziziensis*; and (2) a low-quality group that includes *B. dictyoneura* cv. Llanero and *B. humidicola*. Differences between these two groups appear to be related mainly to protein content.

Animal Production on Pure Grass Pastures

Differences in quality among *Brachiaria* species are reflected in animal performance. In the Brazilian Cerrados (Campo Grande) and the Colombian Llanos (Carimagua), annual LWG was measured in different *Brachiaria* species with no N fertilization. Under similar stocking rates, LWG was lower with *B. humidicola* and *B. dictyoneura* than with *B. decumbens*, *B. ruziziensis*, or *B. brizantha* cv. Marandu (Table 4).

To further illustrate the differences in animal performance among *Brachiaria* species, LWG patterns recorded over several years in grazing experiments at Carimagua are shown in Figures 1 and 2. While LWG on signalgrass pastures stocked with 2 hd/ha remained relatively stable over time (Figure 1), LWG dropped by 100 kg/hd on *B. dictyoneura* and 50 kg/hd on *B. humidicola* when grazed with the same stocking rate over a 5-year period (Figure 2) (C. E. Lascano, unpublished data). Similarly, in grazing studies on the Guadalcanal Plains, Solomon Islands, LWG measured over a 4-year period (high stocking rate: 3.6 hd/ha) declined more on *B. humidicola* (27%) than on *B. decumbens* (21%) or *B. mutica* (19%) (Smith and Whiteman, 1985).

Losses of productivity on *B. dictyoneura* and *B. humidicola* pastures in the Colombian Llanos have been associated with a decline over time in CP level (from 8% to 4%) in the forage on offer of both species and a continuous infestation of spittlebug in *B. dictyoneura* cv. Llanero.

Table 4. Liveweight gain (LWG) of cattle grazing *Brachiaria* pastures with or without N and P fertilization.

Location, soil	Rainfall (mm/year)	Species	Fertilizer	Stocking rate (hd/ha)	Annual LWG (kg/ha)	Average based on years	Reference
Brazil (Campo Grande), Dark Red Latosol	1,500 (5-6 months dry season)	*B. humidicola*	None	2.0	228	5	CNPGC, 1988
		B. ruziziensis		2.0	285	3	
		B. decumbens cv. Basilisk	P	2.5	343	3	Euclides et al., 1993a
		B. brizantha cv. Marandu		2.4	342		
		B. brizantha cv. Marandu	None	2.2	290	6	Bianchin, 1991
Colombia (Carimagua), Oxisol	2,200 (4 months dry season)	*B. decumbens* cv. Basilisk	P	1.8	247	16	C. E. Lascano, unpublished data
		B. humidicola	P	1.9	176	2	Tergas et al., 1982
		B. humidicola	P	2.0	230	6	C. E. Lascano, unpublished data
		B. dictyoneura cv. Llanero	P	2.0	226	5	C. E. Lascano, unpublished data

High levels of CP (10%-12%) in the forage on offer can be obtained in *B. humidicola* and *B. dictyoneura* without N application, through very high stocking rates (Hoyos and Lascano, 1985; Lascano et al., 1991). However, this strategy leads to low forage availability and hence low voluntary intake and low LWG (Hoyos and Lascano, 1985). But, under normal grazing pressure, the low levels of CP in *B. dictyoneura* and *B. humidicola* grown on acid, infertile soils (i.e., the Colombian Llanos) appear to be related to the inhibition of nitrification (Sylvester-Bradley et al., 1988). How far these two grasses can also inhibit nitrification in more fertile soils is not known. Anecdotal evidence suggests that LWG on *B. humidicola* grown on fertile soils in humid areas is relatively stable over time.

Animal production on grass-legume pastures

An effective way to increase the CP content of *Brachiaria* pastures is through grass-legume associations. However, because of the inherent aggressiveness of most *Brachiaria* species, few associated legumes have persisted. Annual LWG in pastures of *Brachiaria* with or without legumes are summarized in Table 5. Results from a short-term grazing study in Campo Grande, Brazil, showed an 18% advantage in LWG from the association of signalgrass with the legume *Calopogonium mucunoides*.

In a long-term grazing trial in the Colombian Llanos, signalgrass associated with *Pueraria phaseoloides* (kudzu) produced, on average, 40% more LWG than the grass alone over the first 9 years of grazing (Lascano and Estrada, 1989). Over a longer period (16 years), the signalgrass-kudzu pasture has produced an average of 34% more LWG than the grass alone (C. E. Lascano, unpublished data). The grass-legume pasture has shown a clear advantage over the pure grass one, giving a 67% higher LWG in the dry season and a 24% higher LWG in the wet season, indicating both a direct (i.e., animal selection) and an indirect

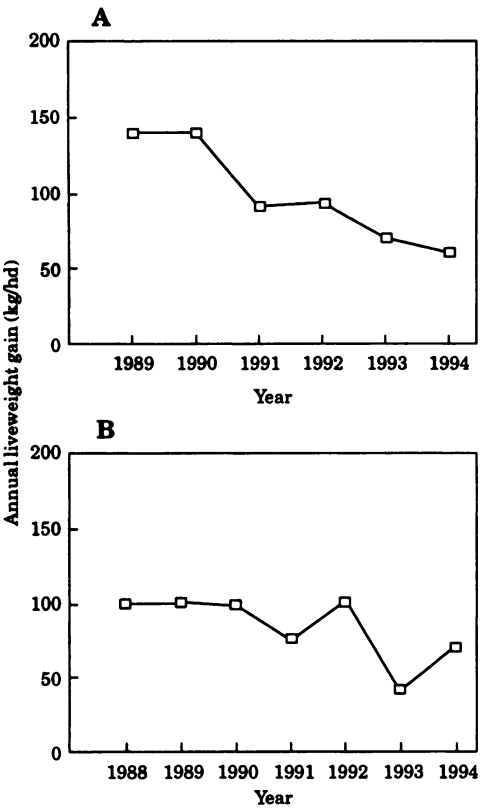

Figure 2. Liveweight gain per head of livestock on *Brachiaria* pastures stocked with 2 head/ha in the Colombian Llanos: (A) *B. dictyoneura* cv. Llanero; (B) *B. humidicola* cv. Humidícola. (C. E. Lascano, unpublished data.)

(i.e., N cycling) contribution of the legume to animal performance (Lascano and Estrada, 1989).

The excellent compatibility and persistence of *A. pintoi* cv. Amarillo with *Brachiaria* was documented in the Colombian Llanos by Grof (1985). Following these initial results, grazing experiments were established in the Llanos and in the humid tropics of Costa Rica to measure LWG on *Brachiaria* with and without *A. pintoi*. Associations gave substantially higher LWG than the pure grass pastures: 67% higher for *B. humidicola*, and 52% higher for *B. dictyoneura*. In the more favorable environment of a humid forest site at Guápiles, Costa Rica, LWG on heavily stocked pastures of *B. brizantha* cv. Marandu/*A. pintoi* has been exceptionally high (Table 5), producing 30% more LWG over a 3-year period than the pure grass. At this site, the pure grass pasture is showing signs of N deficiency (P. J. Argel, 1994, personal communication), which, in the long term, will undoubtedly result in greater advantage in LWG because of the legume.

Another legume compatible with *Brachiaria* is *Desmodium ovalifolium* (now *D. heterocarpon* subsp. *ovalifolium*). In a humid environment of Bahia, Brazil, pastures of *B. humidicola* and *D. ovalifolium* were relatively stable over time with adequate grazing management (Pereira et al., 1992b). However, because of the low quality of the legume (i.e., tannins), LWG on the grass-legume association did not differ from that on the pure grass (Pereira et al., 1992a).

Few studies have measured milk yields of cows grazing *Brachiaria* pastures with or without legumes. In short-term grazing experiments at CIAT's experiment station at Santander de Quilichao (Cauca, Colombia), daily milk yield was greater on signalgrass (8 kg/cow) than in *B. dictyoneura* (6 kg/cow) (C. E. Lascano, unpublished data). At the same location, cows grazing pastures of an association of *B. dictyoneura* cv. Llanero with *Centrosema* species or *Stylosanthes guianensis* each produced 2 or 3 additional kg of milk/day, respectively, than cows grazing a pure grass pasture (Lascano et al., 1991; C. E. Lascano and J. W. Miles, unpublished data).

In general, the literature reviewed in this section indicates that differences exist in quality and animal production among *Brachiaria* species. However, the higher digestibility of *B. decumbens* and *B. ruziziensis*, compared with *B. brizantha*, has not been shown to translate into better animal production. In contrast, low CP levels in *B. dictyoneura* cv. Llanero and *B. humidicola* cv. Humidícola when grown on acid, infertile soils have resulted in low animal

Table 5. Annual liveweight gain (LWG) of cattle grazing pastures of *Brachiaria* with or without legumes.

Location	Species	Stocking rate (hd/ha)	LWG/year		Average based on years	Reference
			(kg/hd)	(kg/ha)		
Campo Grande, Brazil	*B. decumbens*	3.3/4.7, dry/wet season	-	327	3	CNPGC, 1988
(Cerrados)	*B. decumbens*/Calopo	3.3/4.7, dry/wet season	-	385		
Villavicencio, Colombia	*B. brizantha* cv. La Libertad/	3	203	609	3	Pérez and Lascano, 1992
(Llanos-Piedmont)	*Arachis pintoi*					
	B. decumbens/A. pintoi		199	597		
	B. dictyoneura/A. pintoi		180	540		
	B. humidicola/A. pintoi		176	528		
Carimagua, Colombia	*B. decumbens*	2	125	225	3	Lascano and Estrada, 1989
(Llanos)	*B. decumbens*/Kudzu		174	313		
	B. humidicola	2, 3, 4	80	240	6, averaged across stocking rates	C. E. Lascano, unpublished data
	B. humidicola/A. pintoi		134	402		
	B. dictyoneura	2, 3	85	222	5, averaged across stocking rates	C. E. Lascano, unpublished data
	B. dictyoneura/A. pintoi		129	338		
Guápiles, Costa Rica	*B. brizantha*	6	119	714	3	Hernández et al., 1995
	B. brizantha/A. pintoi		154	924		

production, particularly when compared with signalgrass. The poor animal performance on these two cultivars can be overcome to a large extent by growing them in association with a compatible, high-quality legume such as *A. pintoi*.

Quality of lesser known *Brachiaria* species

The forage quality of lesser known *Brachiaria* species was measured as part of the characterization of a large collection of *Brachiaria* germplasm in the Colombian Llanos (G. Keller-Grein, 1994, personal communication). Leaves of different accessions of *B. jubata*, *B. nigropedata*, *B. platynota*, *B. subulifolia*, and *B. subquadripara* planted at Carimagua were sampled during the dry season and analyzed for CP and IVDMD. Average CP (8%) of these species was similar to that of accessions of *B. decumbens* (10%) and *B. brizantha* (9%). However, IVDMD values of *B. nigropedata* (48%), *B. platynota* (53%), and *B. subulifolia* (45%) were low, particularly when compared with *B. jubata* (67%).

To assess further the forage value of some of these lesser known *Brachiaria* species, leaves of accessions of *B. jubata*, *B. nigropedata*, *B. platynota*, and *B. subquadripara* were sampled during the rainy season from the germplasm collection planted at Quilichao (C. E. Lascano, unpublished data). Results show that cell-wall content—neutral detergent fiber (NDF)—of the different *Brachiaria* species (Table 6) is within the range expected for tropical grasses (Minson, 1990). But the IVDMD of *B. nigropedata*, *B. platynota*, and *B. subquadripara* is considerably higher than that of samples taken at Carimagua during the dry season. Results also indicate a certain amount of variability in NDF and IVDMD among accessions (Table 6).

Agronomic performance in terms of tolerance of dry-season stress and of acid, infertile soils is poor in these lesser known *Brachiaria* species at Carimagua (G. Keller-Grein, 1994, personal communication). Under these conditions, forage digestibility is normally low. Therefore, the evaluation of some of these species at locations with moderately acid soils of higher natural fertility is recommended.

Toxicity of *Brachiaria* Species

Several cattle health syndromes have been associated with grazing *Brachiaria* pastures. For instance, the syndrome known as "vaca caída" ("fallen cow") strikes cows grazing signalgrass pastures during late gestation or early lactation. In most cases, the pasture is at least 5 years old. Reports of deaths are common in the Brazilian Cerrados and the Venezuelan Llanos (B. Rosa, 1994, personal communication). The exact cause of the syndrome is still not known,

Table 6. Forage quality of lesser known *Brachiaria* species from the germplasm collection maintained at Quilichao, Colombia.

Species[a]	Number of accessions	NDF[b] (%)	IVDMD[b] (%)
B. jubata	38	70 (53-77)	78 (73-83)
B. nigropedata	22	74 (68-77)	69 (65-73)
B. platynota	3	72 (67-75)	74 (72-76)
B. subquadripara	3	62 (55-65)	77 (76-79)

a. Last expanded leaf.

b. NDF = neutral detergent fiber; IVDMD = in vitro dry matter digestibility; numbers in parentheses are ranges.

SOURCE: C. E. Lascano, unpublished data.

but the saprophytic fungus, *Pithomyces chartarum*; the bacterium, *Clostridium botulinum*; or a mineral nutrient imbalance may be involved. Another syndrome, known as "cara hinchada" ("swollen face") (parathyroidism), occurs in the Brazilian Cerrados in horses grazing pastures of *B. humidicola*. This syndrome was associated with a mineral imbalance (Ca deficiency) that causes oxalate accumulation (Nunes et al., 1990) and with the presence of anaerobic bacteria (B. Rosa, 1994, personal communication).

Nitrate toxicity has been reported in livestock grazing *B. arrecta* (tannergrass), and photosensitization in livestock grazing signalgrass and other *Brachiaria* species. Some of the data on nitrate toxicity and hepatogenous photosensitization associated with *Brachiaria* species are briefly reviewed.

Nitrate toxicity

Toxicity in livestock grazing tannergrass was reported in the early 1970s by several researchers from Brazil (Andrade et al., 1971; Oschita et al., 1972; Rosenfeld et al., 1971). One explanation given is that tannergrass has the ability to accumulate high levels of nitrates in the tissue. For example, Andrade et al. (1971) reported 27 times more nitrate in tannergrass than in signalgrass (0.8% versus 0.03% KNO_3 equivalent). However, a subsequent study showed that, with heavy N fertilization (400 kg/ha), both *B. decumbens* and *B. ruziziensis* accumulated as much nitrate (1,134 to 1,818 ppm) as tannergrass (1,619 ppm) (Queiroz Filho et al., 1982). In the same study, *B. ruziziensis* accumulated more nitrate (1,075 ppm) than tannergrass (694 ppm) at lower levels of N fertilization (200 kg/ha). Nitrate toxicity of livestock grazing N-fertilized pastures of *B. decumbens* or *B. ruziziensis* has not been reported.

The role of different levels or activity of the enzyme nitrogen reductase in determining differences in nitrate accumulation among *Brachiaria* species is unclear. However, under certain conditions (i.e., high soil nitrate concentration, drought, low light intensity), some of the well-known *Brachiaria* species can accumulate toxic levels of nitrate. The conditions under which toxicity occurs need to be determined so to avoid the problem in intensive livestock systems where *Brachiaria* pastures are heavily fertilized with N.

Photosensitization

A widespread, but sporadic, toxicity syndrome associated with *B. decumbens* is hepatogenous photosensitization, which can cause losses in LWG of up to 40% in severe cases (Fagliari et al., 1991). Toxicity symptoms, mainly in young sheep, goats, and cattle, include skin lesions, facial edema, liver damage, ruminal stasis, neurological disorders, and even death if animals are not removed from the pasture (Abas-Mazni et al., 1983; Salam Abdullah et al., 1988; 1989). In most reports from Africa, Southeast Asia, or South America, photosensitization has occurred in animals on signalgrass. However, toxicity has also occurred in sheep grazing mainly *B. brizantha* cv. Marandu (Magalhães et al., 1988) and in horses grazing *B. humidicola* (Schenk et al., 1991).

Photosensitization with signalgrass has been related to infestation of the grass by the saprophytic fungus *P. chartarum*, which produces spores thought to contain toxic sporidesmin (Andrade et al., 1978; Dobereiner et al., 1976; Nobre and Andrade, 1976). However, the cause-effect relationship between *P. chartarum* and photosensitization in signalgrass has been challenged by researchers from Malaysia (Abas-Mazni and Sharif, 1986; Salam Abdullah et al., 1992) and New Zealand (Smith and Miles, 1993). The arguments put forward against the theory that *P. chartarum* alone is responsible for photosensitization in signalgrass are:

1. In South America, different strains of *P. chartarum* were isolated from *Brachiaria* pastures where cattle had exhibited toxicity, but no strain had produced sporidesmin (Brewer et al., 1989).

2. In New Zealand, a high correlation between spore count in the pasture and toxicity (facial eczema) exists in sheep (Brook, 1969), but this does not appear to be the case in South America (E. Aycardi, 1994, personal communication).

3. In Malaysia, sheep developed photosensitivity when fed hay or fresh signalgrass. However, liver damage was not observed when grass litter, ideal for fungal growth, was fed (Abas-Mazni and Sharif, 1988).

4. The pathology of animals poisoned with signalgrass is similar to that found in animals grazing *Panicum* species not infected with *P. chartarum* (Graydon et al., 1991).

5. Steroidal saponins were isolated from the rumen contents of poisoned sheep fed signalgrass (Lajis et al., 1993; Salam Abdullah et al., 1992). In addition, steroidal saponins were identified in several plants known to cause photosensitization (Miles et al., 1993), and the toxicity symptoms were reproduced in sheep through oral dosing of crude saponins extracted from the plant *Tribulus terrestris* (Zygophyllaceae) (Kellerman et al., 1991).

Clearly, more study is needed on the role of steroidal saponins in hepatogenous photosensitization in livestock and their possible interaction with *P. chartarum* and other fungi (endophytes) that may be present in *B. decumbens* and other *Brachiaria* species. Even if photosensitization in ruminants and horses is not caused primarily by *P. chartarum*, the presence of fungal spores may exacerbate the toxicity (Smith and Miles, 1993).

Scope for Improving the Quality of Commercial *Brachiaria* Species

Intraspecific variability in quality

As part of the morphological and agronomic characterization of the *Brachiaria* germplasm collection held at CIAT, differences in quality among accessions of important species are being assessed. Crude protein and IVDMD of four *Brachiaria* species grown in Costa Rica (Guápiles) and Colombia (Quilichao and Carimagua) differed widely (Table 3). Large intraspecific differences of CP were recorded in all *Brachiaria* species evaluated on an Inceptisol in Costa Rica. In contrast, the variability of CP in *B. humidicola* accessions grown on an Oxisol in the Colombian Llanos was considerably less.

Wide variation in IVDMD within *Brachiaria* species was found at all three sites. When averaged across sites, differences between high and low values were 10 digestibility units for *B. ruziziensis*, 14 units for *B. decumbens*, and 20 units for *B. brizantha*. These differences point to ample possibilities of selection for increased digestibility in commercially important *Brachiaria* species.

Relationship between genotype-by-environment interaction and forage quality

Selection for improved forage quality is clearly justified if genetic variance for digestibility or CP is greater than the variance resulting from the interaction of genotype with environment (GxE). To verify this, 20 accessions of *B. decumbens* or *B. brizantha* were planted at three locations in Colombia with contrasting climate and soil (Vertisol at Palmira, Ultisol at Quilichao, and Oxisol at Carimagua). Variance in IVDMD caused by genotype was four times greater than variance from GxE interaction

(J. W. Miles and C. E. Lascano, unpublished data). Similar results were noted by Vogel and Sleper (1994) in a literature review on quality improvement of temperate grasses.

A closer analysis of the data on some *Brachiaria* species showed that, while the IVDMD of *B. decumbens* cv. Basilisk was stable across locations, that of *B. brizantha* cv. Marandu declined by 5 units when grown at the less favorable Carimagua site. This result is probably a reflection of the marginal adaptation of this cultivar to acid, infertile soils.

Selection criteria for improved forage quality

Improvement of protein concentration in *Brachiaria* seems feasible, as indicated by the variation in CP among accessions of some important *Brachiaria* species grown at different sites. However, based on results with other grass species, GxE variance for CP in *Brachiaria* is likely to be greater than genetic variance (Vogel and Sleper, 1994). But, the large variation in IVDMD and the stability of this attribute across environments suggest that digestibility of *Brachiaria* species can be improved. Even small changes in digestibility in *B. decumbens* or *B. brizantha* could have a significant impact on animal performance, as was shown with bermudagrass (Hill et al., 1993).

In a program to improve digestibility of *Brachiaria* species, selection criteria and sampling methods should be clearly defined. Some plant attributes (e.g., cell content relative to cell wall, leaf-to-stem ratio, late versus early flowering) are useful indirect selection criteria for digestibility. Given that the IVDMD changes with the plant's physiological stage, samples must be taken to minimize variation due to stage of growth or flowering. One possibility is to measure the IVDMD in the last expanded leaf of the plant (M. J. Fisher, 1994, personal communication).

Future Research Needs

Based on our review of forage quality and animal production in *Brachiaria* species, we suggest four areas that need attention from researchers:

1. Exploiting differences in digestibility within *Brachiaria* species. Special emphasis should be given to the evaluation of accessions of *B. brizantha, B. decumbens*, and *B. ruziziensis* with high IVDMD values. Accessions of *Brachiaria* species with higher digestibility than commercial cultivars and good agronomic performance on acid soils should be evaluated in grazing trials to assess compatibility with legumes and animal production potential.

2. Maintaining the quality of *Brachiaria* bred lines at least equal to that of *B. decumbens* cv. Basilisk. In breeding programs designed to incorporate spittlebug resistance, selected *Brachiaria* hybrids should be evaluated for digestibility, together with spittlebug resistance, acid-soil tolerance, plant morphology, and seed yield.

3. Understanding the causes of low CP concentration in the tissue of *B. humidicola* and *B. dictyoneura* cv. Llanero grown on acid soils. Quality and animal production over time need to be measured in *B. humidicola* pastures grown on more fertile soils.

4. Determining the causes of toxicity associated with *Brachiaria* species. Research would include (a) determining whether differences exist among and within *Brachiaria* species in nitrate levels and N reductase activity when grown under conditions that favor nitrate accumulation (e.g., high rates of N application, shade); (b) defining more clearly the role of steroidal saponins in photosensitization; (c) screening accessions of *Brachiaria* for steroidal saponins;

and (d) determining the saponins' possible interaction with plant factors (stage of maturity), environmental factors (rainfall, drought, shade), and fungi (*P. chartarum*, endophytes).

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To save space, the following acronyms are used in place of publishers' names:

ASA = American Society of Agronomy

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

CPAC = Centro de Pesquisa Agropecuária dos Cerrados

CSSA = Crop Science Society of America

FAPESP = Fundação de Amparo à Pesquisa do Estado de São Paulo

FEALQ = Fundação de Estudos Agrários "Luiz de Queiroz"

INRA = Institut national de la recherche agronomique

INZ = Instituto de Zootecnia

JSGS = Japanese Society of Grassland Science

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Agricultural Science

NZSAP = New Zealand Society of Animal Production

SCJ = Science Council of Japan

SSSA = Soil Science Society of America

TGSA = Tropical Grasslands Society of Australia

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Chapter 8

Reproductive Physiology, Seed Production, and Seed Quality of *Brachiaria*

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Abstract

Seed of six commercial *Brachiaria* species is extensively produced for pasture sowing. Production is restricted geographically and seasonally by photoperiodic flowering reactions. It also requires a prior control of vegetative tiller production, and therefore a reliable dry season. The necessary conditions are most readily found at high tropical latitudes.

Seed crop management is mostly conventional. Vigorous synchronized tillering is stimulated by decapitation and use of nitrogenous fertilizer at times when rainfall, temperature, and sunshine are expected to favor unrestricted development. Ripe seed sheds readily and, coupled with imperfect synchronization of crop ripening, tends to make conventional direct harvesting inefficient and its timing critical. Where possible, seeds are let to fall and accumulate, and then recovered. Seed yields range from more than 1,000 kg/ha of pure seed to less than 100 kg/ha.

Seed quality is heavily influenced by vitality and dormancy. Vitality depends mostly on maturity of seed at harvest, being higher in accumulated fallen seed and much lower in directly severed seed. Dormancy is strongly developed in the genus and persists in most taxa at least into the season after harvest. This creates problems for germination testing and in the field use of fresh seed. Breaching the husk, most commonly by sulfuric acid, provides a partial solution.

Suggestions are offered for improving seed production when developing new cultivars, particularly for selecting flowering control mechanisms compatible with production at low latitudes.

Introduction

Six taxa of *Brachiaria* are important enough as pasture plants to be grown extensively for seed—*B. decumbens*, *B. humidicola*, *B. brizantha*, *B. mutica*, *B. ruziziensis*, and *B. dictyoneura*[1] as demonstrated in this volume by Argel and Keller-Grein (Ch. 14), Pizarro et al. (Ch. 15), and Stür et al. (Ch. 17). In these chapters and that of Keller-Grein et al. (Ch. 2), the history of these materials is also described. Too little is known of other members of the genus to provide a coherent picture of their reproductive behavior.

Our objective here is to characterize the reproductive properties of the group and identify what may be needed in future cultivars. In this paper, we emphasize:

1. *Brachiaria decumbens*, derived from the Australian introduction CPI 1694 and equivalent to cv. Basilisk (Oram, 1990).

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1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

2. *Brachiaria humidicola* material derived from the Australian CPI 16707 and released as cv. Tully (Oram, 1990).

3. *Brachiaria brizantha*, the Brazilian cv. Marandu (Nunes et al., 1984), is distinct from other, now less important, early introductions, which include the Colombian cv. La Libertad (Ramírez P., 1987).

4. *Brachiaria mutica*, long naturalized in many countries and containing at least some variation (Wesley-Smith, 1973), but no specific cultivar.

5. *Brachiaria ruziziensis*, an apparently uniform type, formerly very widely distributed (Barnard, 1969; Serrão and Simão Neto, 1971; Stür et al., Ch. 17, this volume).

6. *Brachiaria dictyoneura*, introduced as CPI 59610 to, and widely evaluated by, CIAT, was released as cv. Llanero in Colombia (ICA, 1987).

Reproductive Physiology

All *Brachiaria* species may be propagated both vegetatively and from seed. Vegetative propagation is simple, but, except in very small-scale farming, impracticable. Here, we consider only reproduction from seed.

All taxa are derived from collections, each perhaps of single plants, made from wild populations, mainly in tropical eastern Africa. Because only the source of supply, and not the point of collection, is normally given in cultivar descriptions, our material cannot be readily related to a background of either local adaptation or original population diversity. Rationalizing reproductive behavior in terms of natural adaptation is therefore difficult.

The study of reproductive processes in *Brachiaria* has been influenced mostly by agronomic research needs to rationalize flowering behavior. Although such research, from a physiological viewpoint, has been superficial, it has provided a working framework that can be used, with caution, until more complete information becomes available.

Inflorescence development

A young plant will not initially produce inflorescences; to explain this, some form of juvenility is usually inferred. An inflorescence population developing from a seedling sward is slow, sparse, poorly synchronized, and of little practical value. Reproductive development is therefore best viewed as starting with the proliferation of tillers in an established sward. In all taxa, this is stimulated both by the decapitation of existing tillers and by an abundance of available soil N. Such effects are widely observed in grasses, but still poorly understood (Murphy and Briske, 1992). Decapitation is effective, perhaps because apical dominance is removed and light penetrates better to bud sites. The two influences are exploited together to produce the dense population of similarly aged tillers, which, if subsequent conditions for growth and floral differentiation are favorable, will develop into the seed crop.

The conditions required for growth of tiller populations are ample, continuous supplies of freely available soil moisture, mean daily temperatures above 23 °C, high levels of solar radiation, and soil nutrients (especially N) in sufficient quantities for rapid pasture growth. Under such a combination of conditions, tiller populations rapidly grow to a density at which they inhibit further recruitment, thus producing a discrete burst of development—the basis of the relatively closely synchronized population of inflorescences that constitutes the conventional seed crop.

Flower initiation also has specific photoperiodic needs, which differ among species and restrict both the latitude and time of year at which vigorous flowering may occur. The fragmentary evidence available 10 years ago (Ison and Hopkinson, 1985) showed *B. mutica* to be

an obligate short-day plant, and *B. ruziziensis* to be a quantitative short-day plant, both flowering with enough vigor for useful seed production only after the autumnal equinox in the high tropics and subtropics. *Brachiaria decumbens*, *B. humidicola*, and *B. brizantha* were inferred to be quantitative long-day plants, flowering everywhere in the longer days of the year, and more vigorously at high than at low tropical latitudes. *Brachiaria dictyoneura* cv. Llanero has since been shown to behave similarly (CIAT, 1986; Diulgheroff et al., 1990; Vela et al., 1991; M. Sánchez, J. E. Ferguson, and A. Ortiz, unpublished data).

Flower initiation in individual tillers is sometimes inhibited even when daylength favors it. For example, apices of tillers of *B. humidicola* that emerge into an existing dense sward, either of vegetative tillers or of stubble, are apt to remain indefinitely vegetative. This makes it almost impossible to take more than one crop in a season, and even then difficult, unless the sward is razed. The same effect is apparent in other species to variable, although usually lesser, degrees, especially in climates where temperature and rainfall are such that vegetative growth continues unchecked throughout the year. Stür's analysis (1985) of seed crop development in *B. decumbens* suggests that, among other symptoms of competitive suppression, late-emerging tillers are slower than early ones of the same population to reach inflorescence exsertion, and more likely to remain indefinitely vegetative (Stür and Humphreys, 1987). If tillers of the same population, emerging only 5 days apart, can interfere with one another's reproductive potential, then similar competitive forces may explain why much older and bigger tillers suppress emerging tillers.

Flower initiation is followed by inflorescence differentiation and emergence. Stür (1986) recorded the course of differentiation in *B. decumbens*, which is believed to be similar in major details to that in other species. The initially vegetative shoot apex elongates, initiates racemes, and degenerates. The racemes develop "ridges," which differentiate into spikelets, which then differentiate into floral parts. The whole process is rapid. Floral initiation may occur within 6 days of tiller emergence, spikelet differentiation may start within 10 days of flower initiation, and first inflorescences may emerge about 4 weeks later (Stür and Humphreys, 1987).

The cessation of tiller emergence and the weaker development of late-emerging tillers brings the phase of inflorescence emergence to a close. It lasts a variable time—Stür (1985) recorded it as 28 days—and largely sets the pattern of spread over time of crop ripening. The density of emerged inflorescences is the main determinant of spikelet density; hence, of potential seed formation. Potential inflorescence density differs among taxa, being highest in *B. humidicola*, sometimes approaching 2,000/m^2; intermediate in *B. decumbens*, *B. dictyoneura*, and *B. ruziziensis*, in which it commonly reaches 700-1,000/m^2; and lowest, at about 200/m^2, in *B. brizantha* (Andrade et al., 1983; Stür, 1985; present authors, unpublished data).

Seed development

After inflorescence emergence anthesis of spikelets occurs. Anthesis on a single head, and between heads in a population, is staggered over time, although not enough to significantly affect the overall spread of crop ripening. Pollination is required, whether seeds develop sexually or apomictically (Valle and Savidan, Ch. 10, this volume). *Brachiaria ruziziensis* is sexual, the others are predominantly apomictic (Ferguson and Crowder, 1974; Pritchard, 1967; Valle, 1986; 1990). How dependent the success of seed set (the formation of a recognizable caryopsis) in the crop is on the influence of either apomixis or the genetic irregularities associated with polyploidy (Sotomayor-Rios et al., 1960) is, so far, impossible to assess. Also usually difficult is to equate caryopsis contents of

samples with success of pollination, because discrimination is seldom possible between preanthesis and failed-set spikelets in the empty fraction. Caryopsis contents rarely exceed 30% (Stür, 1985; F. H. D. de Souza and J. M. Hopkinson, unpublished data), and overall seed set of the heaviest yielding crops of, for example, *B. decumbens*, is unlikely to exceed 40%. But the importance of the various possible genetic causes of such failure remains open to conjecture.

Failure of seed set has other, more tangible, causes too, the commonest being drought stress in the crop at anthesis. This is conspicuous in *B. humidicola* in Australia in dry years, and is probably common in both *B. decumbens* and *B. humidicola* growing on sandy soils in Thailand (W. W. Stür, 1994, personal communication). Seed set of *B. humidicola* fails consistently in Colombia, despite prolific flowering and abundant moisture (J. E. Ferguson, 1994, personal communication). Similar failure was recorded in *B. brizantha*, *B. decumbens*, and *B. dictyoneura* at 6° 30' N in Antioquia, Colombia (Osorio et al., 1991). This kind of behavior raises the possibility of photoperiodic response varying with stage of development, for which precedents exist among other warm-climate grasses (Ison and Hopkinson, 1985).

Caryopsis development follows seed set. The caryopses of all *Brachiaria* species reach a finite size at maturity that varies only within narrow limits and is set by the dimensions of the husk, which remains remarkably constant within any taxon. In this respect, *Brachiaria* species are like other tight-husked panicoid grasses, contrasting with those whose caryopses, not being enclosed in rigid structures, can vary greatly in size at maturity (e.g., species of *Chloris* and *Cenchrus*, and many Andropogoneae).

The attainment of maturity, without which high seed vitality cannot exist, apparently depends largely on the rate of growth of the caryopsis, relative to the rate of development of the abscission layer. In the similarly structured *Panicum maximum* seed, the time taken for the abscission layer to develop is relatively constant, whereas the time taken for the caryopsis to mature is variable and dependent on seasonal weather (Hopkinson and English, 1982c).

This conclusion may apply equally to *Brachiaria*. Cool weather or prolonged overcast periods, for example, retard caryopsis growth, with the risk that abscission will precede maturation in a high proportion of spikelets. This results in abnormally high proportions of immature seeds even at harvest ripeness, inevitably reflected in the condition of the harvested seed. Variation in immature seed content is a major cause of differences in seed quality between districts or seasons. An immature caryopsis, besides being itself incompletely developed, fails to occupy its husk cavity fully. Because the seal between the lemma and palea depends on their overlapping parts being forced together by the final growth of the caryopsis, and because the protective capability of the husk depends on a tight seal, a secondary effect of immaturity is defective protection against rapid entry of foreign bodies such as water or fungal hyphae. This leaves immature seed vulnerable to damage and disease, as well as physiologically weak.

The extent of maturity of a population of pure seeds is easily judged from a measure of the average pure-seed spikelet weight, the reliability of the figure being dependent on the uniformity of spikelet dimensions. In *B. decumbens* cv. Basilisk, for example, <450 mg/100 seeds indicates a low, 450-500 a moderate, and >500 mg/100 a high level of maturity. Mature seed weights for other taxa are about 650 mg/100 for *B. brizantha*; 500-650 for *B. ruziziensis*; 400 for *B. humidicola*; 110 for *B. mutica*; and variable in *B. dictyoneura* cv. Llanero, 480-550 being recorded under some conditions, 560-620 under others (Diulgheroff, 1991; Phaikaew et al., 1993; present authors, unpublished data).

Seed retention

Abscission is common to all commercial *Brachiaria* species. It occurs shortly after gross physical development (but not every detail of maturation) is complete, and thus results in brief peaks in the quantities of seed retained on the crop. Prolonging retention apparently does little to improve seed recovery efficiency. As the abscission layer is between the glumes and the pedicel, methods tried with other grasses to improve retention, such as spraying with adhesives or selecting plants with tightly enclosing glumes, offer little hope. Individuals or populations with faulty or delayed abscission have not been found so far.

All the events so far described influence the pattern of retention of ripe seed on the standing crop. This has been much measured, being central to harvest strategy, and is highly variable. Individual taxa, however, have characteristics recognizable through the mass of other variations. Seed ripening tends to be the most closely synchronized in *B. humidicola*; intermediate in *B. decumbens*, *B. dictyoneura,* and *B. ruziziensis*; and least in *B. brizantha* commercial cultivars.

Seed Production

The capacity to produce cheap, abundant, high-quality seed is crucial to the widespread adoption of a pasture cultivar. This has been demonstrated many times in the history of *Brachiaria*. For example, the value of *B. decumbens* was known in Queensland in the 1940s (Schofield, 1944), yet its adoption was delayed until the 1960s, when a combination of factors—realization of the existence of dormancy (Grof, 1968), discovery of suitable seed-growing districts, and use of combine harvesters—stimulated the first large-scale seed production. Similar trends of events have since been repeated in other species. A recent example is the adoption of cv. Llanero in Colombia, resulting from successful local seed production, after the failure of seed production in otherwise useful species (ICA, 1987; M. Sánchez et al., unpublished data).

Local seed production is usually preferred, and is sometimes the only possible course, but importation is an option for many countries, and, as a result, a substantial world trade in seed has developed. The main exporters are Brazil (to other tropical American countries [Santos Filho, Ch. 9, this volume]) and Australia (to the western Pacific and Southeast Asia [Stür et al., Ch. 17, this volume]).

The original focus of seed production, in the early 1970s, was Australia, with *B. decumbens*. This helped set in motion the massive expansion that took place in Brazil a few years later and made Brazil by far the dominant producer. Since then, the choice of species has widened, and their use increased; many other countries now produce seed. Table 1 lists recent production records, although these may be incomplete because of a lack of information.

Success in seed production comprises four major elements: locality for growing the crop, crop management system, harvesting method, and attention to the problems of seed quality. Of these, the first is of overriding importance: if this choice can be correctly made, then the complications of the others are greatly reduced. Harvesting method, although influenced by the first two, is essentially governed by economic rather than biological factors, particularly by the relative availability of capital and labor.

Choosing a locality for seed production

There is economic incentive to produce seed wherever a pasture or fodder crop sward is successful. Geographical limits to pastoral use are discussed in other contributions to this volume (Fisher and Kerridge, Ch. 3; Keller-Grein et al.,

Table 1. Estimates of recent annual seed production of commercial *Brachiaria* species.[a]

Region or country	Seed production (t/year)[b]					
	bri	dec	dic	hum	mut	ruz
Australia	0	150	0	50	2	0
Tropical America						
Bolivia	10-20	10-20				
Brazil	40,000	40,000		>500		100-400
Central America and Mexico	5-10	5-10	5-10			
Colombia		20-50	10-20			
Cuba		10-20				
Peru		10-20				
Venezuela	50	50		50-100		
Asia						
India						40
Thailand						450-630

a. Gaps denote lack of information.

b. Species: bri = *B. brizantha*; dec = *B. decumbens*; dic = *B. dictyoneura*; hum = *B. humidicola*; mut = *B. mutica*; ruz = *B. ruziziensis*.

SOURCES: Tropical America, excluding Brazil: CIAT, 1990; Brazil: F. H. D. de Souza, estimated data; India: Kerala Livestock Development Corporation, unpublished records; Thailand: Phaikaew et al., 1993; Phaikaew and Pholsen, 1993; Australia: J. M. Hopkinson, estimated data.

Ch. 2). They are set climatically, primarily by limits of adaptability to low temperatures and low rainfall, and, in the Americas, by the severity of spittlebug predation. Within these limits are environmental requirements specific to seed production.

The first requirement is to match conditions that favor unrestricted crop growth with daylengths that satisfy photoperiodic needs for vigorous flowering. This applies to all taxa equally, their specific and differing requirements being largely a reflection of their different photoperiodic responses.

Within any one country and for any one taxon, achieving this match depends on the range of latitudes and climates available. It is most readily met for long-day taxa when they are grown as summer crops at high tropical latitudes in districts with a reliable summer wet season, while the short-day plants in the same places depend on the continuation of both rainfall and warm temperatures into the tropical "winter."

The greatest difficulties arise at low latitudes, where the period of long days is too short to promote vigorous flowering in long-day taxa. A clear example comes from Colombia, where at about 5° N, *B. humidicola* flowers but fails to set seed, and seed production of *B. decumbens* and *B. brizantha* is very low. Only *B. dictyoneura* cv. Llanero flowers and sets seed vigorously enough to permit commercial seed production, which has been of critical importance to its adoption there (Sánchez and Ferguson, 1992). Improvement of seed production with increasing latitude is difficult to judge with accuracy, because of the influence of confounding factors, such as low soil fertility. In Peru, at 6-8° S, for example, yields of long-day taxa are low, possibly for other reasons (Vela et al., 1991). Their potential is undoubtedly better at 10° N, judging by the successes in Costa Rica (Diulgheroff et al., 1990; Sylvester-Bradley and Ferguson, 1993).

The second requirement, which applies particularly to the long-day taxa, is to prevent the inhibition of flowering by a continuously dense vegetative sward (see p. 125-126). This is most easily achieved under conditions where drought curtails vegetative growth. Drought also

appears to improve subsequent synchrony of tiller growth, presumably both by reducing sward density and by allowing soil N to accumulate, leading to its later sudden release in abundance when the drought breaks. Hence, a distinct, reliable dry season immediately before the main seed cropping period would be useful.

Suitable combinations of photoperiod and rainfall distribution occur between about the tenth parallel and the Tropic in either hemisphere, and the most successful seed-growing regions are located in these regions.

Once these two needs are satisfied, other specific climatic details can be taken into account. Although production is possible under a wide range of conditions, it is efficient only in part of that range. Relevant factors are mostly local, such as the risk of loss from prolonged wet weather at harvest. But, if seed production is to be commercially viable, the seed function must combine with other uses, such as grazing, hay, and rotation, which make other demands on the plant and emphasize its need to be well adapted to soil conditions and climate. Because the optimal combination of all factors is different for each taxon, a geographical mosaic of suitability tends to occur, in which different districts favor different seed crops. Even this may change with time as patterns of factors change and demand fluctuates.

Market forces tend eventually to reduce seed prices to levels that eliminate production in less-favored districts. This happened, notably, in Queensland in the 1970s, when *B. decumbens* seed production boomed as both domestic and export markets grew, and led to sowings under a very wide range of conditions. It resulted in a shift of production from tropical (18° S), high-rainfall (3,000 mm) districts on the coast to adjacent drier (1,300 mm), upland areas in which yield and seed quality were greatly improved. Thus, sale prices fell to levels that were uneconomic in the less productive districts. Similar effects also dictate the pattern of seed production in the vastly more extensive and less abruptly variable region of central Brazil where seed is grown. There, most seed is produced in northern São Paulo state, in two relatively restricted localities: Auriflama, which favors *B. brizantha* cv. Marandu, and Brodosqui for *B. decumbens* cv. Basilisk.

Those countries that need seed but have no suitable seed-growing districts usually lie at low latitudes or are island states too small for much climatic variation. Their choices, then, are to import seed, seek alternative grasses, or accept low, unreliable seed yields.

Crop management

Most seed production of *Brachiaria* is purposeful, as distinct from opportunistic, as it is with many extensively grown grasses. The exception is *B. mutica*, which commonly grows on land too wet to be reliably harvested and where preharvest management is likely to be wasted. Even this taxon, however, responds to planned management when this is possible.

Once the match with the environment is obtained, seed crop management becomes a matter of aiming for the development of the highest density of seed heads in as close a synchrony as possible. This is done by the long-established method of cutting back the sward and applying nitrogenous fertilizer (see p. 125).

The need for synchronization of seed ripening depends on the harvesting method. If harvesting is done by a single act of severing the seed from the plant, then synchronization is important. If, however, harvesting is done by repeatedly collecting shaken-off seed (Phaikaew et al., 1993) or of accumulated fallen seed, synchronization is less important. Even with the first method, improving synchronization is not necessarily desirable beyond a certain point. Spread over ripening time, while reducing the maximum yield potential, provides some

insurance against misfortune at peak ripeness and some flexibility in the management of large areas of crop. *Brachiaria humidicola,* in particular, is already tightly synchronized under conventional management, often allowing for no more than 3 days for mechanized harvesting before too high a proportion of the crop is shed. The next most closely synchronized are, in order, *B. dictyoneura* (Diulgheroff, 1991), *B. ruziziensis* (Kowithayakorn and Phaikaew, 1993), and *B. decumbens*. Although they are less vulnerable, 50% of their standing pure seed is apt to fall within a week of peak production. *Brachiaria brizantha* cv. Marandu is so poorly synchronized that a single cut of the standing crop will yield only about 10% of the potential, and even that is of poor quality.

The competitive vigor of *Brachiaria* species generally prevents weeds from invading, except during establishment. Even so, *Brachiaria*'s remarkable tolerance of the herbicide atrazine makes most weed control possible (Hawton, 1980). Diseases and pests present few problems specific to seed crops (Valério et al., Ch. 6, this volume). In Australia, a fungal disease—a false smut, *Ephelis* sp. (J. L. Alcorn and R. D. Davis, 1994, personal communication)—reduces seed yield of *B. humidicola*. In Brazil, an ergot, *Claviceps sulcata* (Fernandes et al., 1992), reduces both yield and—through its sticky exudate—efficiency of recovery of *B. decumbens*, especially in late crops. Its extent and severity is such as to warrant investigation of control strategies. Throughout the American tropics, spittlebugs may affect seed crops, especially those of *B. decumbens*, although the pest's significance is as yet unmeasured. A native field rat occasionally causes massive crop losses in Australia, severing the inflorescences to get at the seeds.

Recognition of ripeness

For those crops whose seed must be severed, much attention has been paid in the literature to recognition of ripeness and to the usefulness of measurable characters for identifying the point of maximum seed retention to determine optimal harvest time (Condé and Garcia, 1983; Gonçalvez et al., 1980; González, 1987; Kowithayakorn and Phaikaew, 1993; Oliveira and Mastrocola, 1980). Such literature educates the reader in the dynamics of crop development, but tends not to produce commercially useful criteria. Crops are too variable and the factors too numerous for rule-of-thumb methods to be appropriate. Decisions continue to depend on intuitive integration of these factors through experience, observation, and an understanding of the variable dynamics of the system. However, such decisions become irrelevant when shed seed is to be harvested.

Harvest

Many harvesting methods are used, each matched to the economics and balance of labor to capital of the farming system in which it is used. In small-scale systems, with cheap manual labor, seed may be repeatedly shaken from the heads by hand, or heads may be tied into "living sheaves" for seed to accumulate, or the heads may be hand-cut and "sweated" to loosen the seed before separation (Kowithayakorn and Phaikaew, 1993). In large-scale systems, with cheap labor and a reliable dry season, as in parts of Brazil, seed of *B. decumbens* and *B. brizantha* is allowed to fall and accumulate on the ground, from which it is later swept up by hand (Souza, 1991; Santos Filho, Ch. 9, this volume).

For intermediate levels of production scale and mechanization, tractor-mounted beater systems have been designed (Ramos, 1991), which selectively recover mature seed, although at a relatively low proportion overall (30%-40%) of the standing crop (Cardozo et al., 1991). In capital-rich systems, such as in Australia, crops are either combine-harvested, with the attached standing seed being taken conventionally as if it were a grain crop (*B. humidicola* and formerly *B. decumbens*), or the seed is allowed to fall and accumulate on the leaf mat of a

heavily fertilized sward before being gathered with the cutter bar close to the ground (*B. decumbens*) (Hopkinson and English, 1982b). The development of this method and the yield increases it brought are detailed by Hopkinson and Clifford (1993).

Harvest efficiency, an important issue with many seed crops, has received little attention with *Brachiaria*. It acquires most significance in crops in which the standing seed is direct-combined, that is, primarily *B. humidicola* in Brazil and Australia, and, to a lesser extent, other species in both countries and Colombia. Records of harvest efficiency in such crops are sparse. Hopkinson and English (1982a) recovered, on the average, more than 80% of standing seed of *B. decumbens*, although only about 30% of total seed present. Cardozo et al. (1991) combine-harvested an average of almost 50% of what was available for hand harvesting in *B. dictyoneura* cv. Llanero crops.

Seed processing

All seed recovered directly from the crop must be dried after harvest because moisture contents can be as high as 60%, and the usual target for storage is about 10%. Rapid drying can be harmful, apparently because final maturation continues after severance (Hopkinson et al., 1988). Many methods of drying are used, from simple sun-drying on hard surfaces to bin-drying with forced drafts of warmed air.

Undried seed is, metabolically, still highly active, and if packed tightly in bulk, as with all combine-harvested seed, may be unable to dissipate heat and waste gases generated by metabolism. Accumulation of either or both is rapidly fatal to seed. Measures must therefore be taken to ventilate such bulks if drying is delayed, and failure to do so is a frequent cause of lowered quality.

Provided suitable facilities exist, drying, cleaning, and storage present few technical problems. That is, difficulties usually stem from deficiencies in available technology rather than from any peculiarities of the plant. Drying and safe storage under wet tropical conditions is difficult for small farmers without capital. In Brazil, the combination of mechanized harvesting of large areas of *B. humidicola* with open-air drying and casual bulk handling of seed leads to much deterioration. This has given the crop an otherwise undeserved reputation for low seed quality.

Seed yields

Yields of pure seed are highly variable, and have meaning only within their specific context of locality, management system, and harvesting method. As tropical pasture grasses, all *Brachiaria* taxa are potentially high-yielding, but most crops fall well short of their potential. Restrictions on choice of environment and management options, harvest inefficiency, and unreliable weather are the main contributors to the shortfall.

Brachiaria decumbens in Queensland occasionally reaches 1,000 kg/ha of pure seed when accumulated fallen seed is combine-harvested under optimal conditions, but the commonest range for a specialist would be 300-800 kg/ha per crop, with one, sometimes two, crops per season. A standing crop conventionally combine-harvested seldom exceeds 300 kg/ha per crop. Expected yields of swept-up crops of *B. decumbens* and *B. brizantha* in Brazil are about 1,000 kg/ha; those of combine-harvested crops, much lower. Hand-cut and sweated crops of *B. decumbens* in Costa Rica yield 70-150 kg/ha of pure seed, and of *B. brizantha* 60-90 kg/ha, while at lower latitudes, as in Colombia, both species tend to produce considerably less (present authors, unpublished data).

Brachiaria humidicola in Australia occasionally exceeds 400 kg/ha of pure seed with direct combine-harvesting, but records of 20 closely monitored crops gave an average of only 140 kg/ha for harvested

crops and a 30% risk of no harvest, figures that reflect the great risk of loss with this crop (B. H. English and J. M. Hopkinson, unpublished data). Rayman (1981), referring to extensive harvesting in Brazil, quoted 80 kg/ha of seed as an average. In Costa Rica, 50-160 kg/ha is the usual range (S. Diulgheroff, unpublished data).

Yields of *B. ruziziensis* from northeast Thailand are quoted as 300-500 kg/ha of high-quality seed harvested by the "living sheaf" method; and 150-250 kg/ha by cutting and sweating (Phaikaew and Pholsen, 1993; Phaikaew et al., 1993). Few useful figures exist on yields of *B. mutica*. A token 20 kg/ha of saleable seed is expected from unmanaged combine-harvested crops in Australia, but a much greater potential clearly exists.

For Costa Rica, Sylvester-Bradley and Ferguson (1993) report 230 kg/ha of cleaned seed of cv. Llanero in one season, while others quote a range of 120-425 kg/ha (Diulgheroff et al., 1990; Pizarro et al., 1989). A report of 120 kg/ha comes from Ecuador. Numerous records from Colombia exist, with recent, commercial, combine-harvested averages of about 27 kg/ha pure seed, with the best single crop yielding 122 kg (Sánchez and Ferguson, 1992). In a comprehensive series of trials over several seasons and sites, Cardozo et al. (1991) averaged 87 kg/ha pure seed with hand harvests and 48 kg with a combine harvester.

Seed Quality

Conventionally, seed quality has three components: genetic, physical, and vital. Technically, high standards of genetic and physical quality in *Brachiaria* seed are relatively easy to maintain. Vital quality, however, is beset with technical pitfalls that require detailed attention.

Vital quality has two sides: vitality of the seed, that is, its vigor and viability, and the unrelated property of dormancy, which affects planting value and complicates the measurement of vitality.

Vitality

High levels of vitality can be attained only if the seed has the opportunity to mature thoroughly. It thus depends on both the environment for crop growth and on the harvesting method. Immaturity through premature abscission, as earlier described, is common only when the environment is faulty, that is, when the crop is grown at the wrong time of year, in the wrong place, or in a difficult year. Thus, immaturity is only an occasional issue in successfully established seed-growing areas. Its occurrence otherwise suggests the need for close scrutiny of the crop's environment. A certain level of immature seed, often about 30%, is an inevitable component of seed harvested by severance—a consequence of the imperfect synchronization of ripening—whereas fallen seed is predominantly fully mature. This is one reason why swept-up seed is of better general quality than direct-combined seed in Brazil, and why most seed of *B. decumbens* is of higher initial quality than seed of *B. humidicola*.

The retention of vitality, as distinct from its attainment, depends first on preventing damage (whether by pests, diseases, threshing, overheating, suffocation, or rapid drying after harvest) and then on minimizing deterioration during storage.

Mechanical damage by threshing is severe only in crops that have to be threshed vigorously to detach the seed. Combine-harvested *B. humidicola*, in particular, suffers from this kind of damage. As a result, its seed tends to have a reduced dormancy but a shortened storage life. Other forms of damage reflect mostly inexperience, diminishing as industrial sophistication grows.

Deterioration with time is universal. *Brachiaria* seeds are orthodox: their rates of deterioration rise with increase in storage temperature and moisture content (Roberts, 1986). They therefore behave like other similarly structured seeds, and the equation derived to quantify the

course of deterioration in barley seeds in relation to temperature and moisture (Ellis and Roberts, 1981) provides at least an interim working prediction of deterioration in *Brachiaria* seeds. Because they are grown, used, and stored in warm, humid climates and because they readily regain moisture from the atmosphere, *Brachiaria* seeds are prone to rapid storage deterioration. Measures can be taken, however, to mitigate this. While details depend on the practicalities of a given system, attention must first be paid to moisture content, even before temperature, as it is the more critical of the two variables over the normal range of variation, and the cheaper to control. Moisture content is especially important with seed cut directly from the plant, and of least concern with seed swept up in the dry season; such seed may be taken from the field with as little as 5% moisture.

Dormancy

Seed dormancy occurs in all groups of domesticated tropical pasture grasses, but is most conspicuous in those closely related genera of the Paniceae—including *Brachiaria*—whose caryopses are enclosed within a hard, tight husk. The husk, formed by the overlapping lemma and palea of the fertile floret, itself contributes to dormancy. Both husk and dormancy are particularly strongly developed in *Brachiaria*.

Dormancy has an obvious value for seed survival in the savanna ecosystems where most of these plants originated. Under domestication, it is both useful and troublesome. In seed production, it prevents germination in seed of *B. brizantha* and *B. decumbens* in the often-long interval between shedding and harvest. In sward establishment, it may delay emergence and even cause failure if the seed is too fresh when sown; however, it also serves to stagger germination over time, thus reducing risks of total failure under conditions of erratic rainfall. In seed testing, it is an unmitigated nuisance.

Normally all mature, undamaged seed is deeply dormant when newly harvested. As time passes, an increasing proportion of seeds lose their dormancy or become amenable to dormancy-breaking treatments. But also as time passes, the same seed ages: individuals die and survivors lose vigor at rates that vary with storage conditions (Ellis, 1988). The course of dormancy loss also varies, but in ways that are not yet understood. Percentage of germination tends to rise with time to a peak as dormancy weakens, then falls progressively as aging takes increasing effect. While the pattern is general, the timing of events and magnitude of the peak are widely variable. Under conventional storage and testing, the peak may be reached within a few months up to several years after harvest.

Dormancy in *Brachiaria* is imposed physically by the seed coverings and physiologically by embryo dormancy. The former is overcome in testing by removing, or sometimes merely by breaching, the husk (Renard and Capelle, 1976; Whiteman and Mendra, 1982). Acid scarification is the commonest method of breaching the husk, both in routine testing and in treatments for sowing (Castiblanco and Mendoza, 1985; Diulgheroff, 1991; Grof, 1968; ISTA, 1985; Macedo et al., 1994; McLean and Grof, 1968; Magalhães and Groth, 1992). Embryo dormancy presents greater difficulties. It diminishes progressively with age, and, although occasionally absent from fresh seed (Whiteman and Mendra, 1982), it typically inhibits germination in the early months after harvest. Numerous treatments may partially overcome it in testing. They include imbibing seed in potassium nitrate solution and exposing it to, for example, a range of oxidizing agents or plant hormones, temperature fluctuations, light of certain qualities, and dry heat (Atalla and Tosello, 1979; Castiblanco and Mendoza, 1985; Diulgheroff, 1991; Ellis et al., 1986; Goedert and Roberts, 1986; Oliveira and Mastrocola, 1983; Ortiz de

Acosta, 1984; Rodrigues, 1983; CIAT Seed Biology Section, unpublished data).

The significance of dormancy differs with species and circumstances. It is more of a problem in seed testing than in field establishment. It is of little concern with *B. mutica* and *B. ruziziensis*, and, apart from rare exceptions, is short-lived in *B. humidicola* (Atalla and Tosello, 1979; Macedo et al., 1994; Magalhães and Groth, 1992; Oliveira and Mastrocola, 1983). For *B. decumbens*, the tetrazolium viability test permits bypassing the dormancy problem during quality assessment of fresh seed. Of all species, *B. dictyoneura* cv. Llanero shows the most intransigence, with embryo dormancy lasting for as long as 2 years, and husk dormancy making acid scarification, necessary even for field use (Sylvester-Bradley and Ferguson, 1993). Both acid treatment and potassium nitrate are recommended for germination testing, but are only partially effective, except after very long periods of storage (Diulgheroff, 1991).

Except for *B. dictyoneura* cv. Llanero, dormancy is now seldom an issue for field establishment, probably because most farmers know to avoid using fresh seed for sowing. In Australia, acid treatment of *B. decumbens* was abandoned many years ago after it was shown to have no consistent benefit (Hopkinson, 1993). It was never used with *B. humidicola*, which is threshed so hard at harvest that husk damage substitutes for acid scarification. In Brazil, acid treatment to hasten establishment is restricted to *B. humidicola*, although most export seed of any species is still treated to meet quarantine requirements of importing countries. Brazilian farmers mostly use the sweeping-up method of harvesting for *B. brizantha* and *B. decumbens*. Such seed has weathered from lying in leaf litter, losing dormancy in the process, and thus making treatment unnecessary. In *B. mutica*, dormancy does not hinder the emergence of even relatively fresh seed (McLean and Grof, 1968), and, in Australia, dormant seed is never acid treated. *Brachiaria ruziziensis*, likewise, is sown untreated in most countries where it is used.

Conclusions

Availability of abundant, cheap, high-quality seed is necessary, and will continue to be necessary, to support widespread use of current and future *Brachiaria* cultivars. Despite international trade in seed, local production will remain the preferred option. Hence, potential cultivars should be evaluated for their seeding capacity, as well as their usefulness as pasture plants, in the same geographical area.

The most striking aspects of *Brachiaria* seed production are the geographical variation in which success occurs, and the fact that seed production of a species may fail where it is valued as a pasture plant, especially at low latitudes. Photoperiodic flowering reactions seem to be largely responsible for this situation. If, in the development of new cultivars for specific regions, photoperiodic compatibility could be ensured, problems in seed supply may be greatly reduced. Ecotypic variation in photoperiodic response is common in grasses with a wide natural distribution (Foster, 1962; Tothill, 1966). It probably occurs in *Brachiaria* species too. If so, it may be possible to select or even breed for appropriate reproductive behavior during new cultivar development. The chief problem may be to reconcile improved seeding with high pasture quality, the two being, to some extent, mutually exclusive.

Another area of research is the inhibition of flowering by existing tillers, not only in *Brachiaria*, but also in the many other grasses in which it occurs. However, answers are likely to be both slow—it is a problem that has puzzled plant scientists since early days (Murphy and Briske, 1992)—and academic, without providing solutions to agronomic problems.

Within suitable environments, *Brachiaria* species are remarkable for their

success as seed crops. In the absence of market distortions, their seed is accordingly cheap. Shortfalls in supply occur, but seldom because of deficiencies in the plant. The incentive to look for fundamental improvements in seeding properties of the heavier yielders is weak. For example, a simple analysis of production costs of *B. decumbens* in Australia shows that improvement through increased seed yield beyond 1,000 kg/ha is not cost-effective, because the cost reductions that derive from greater yields are too small, relative to the fixed costs per kg of seed produced.

An improvement sometimes suggested is to prolong retention of ripe seed on the standing crop. Although the need for it has been circumvented in some species and under some circumstances, the genetic manipulation of abscission may be particularly useful for *B. humidicola*. Genetic variation in the extent of separation after formation of an abscission layer has been found in *Panicum coloratum* (Young, 1986), but, apart from some grain crops domesticated in ancient times, no tropical grass has been bred or selected for greater seed retention. If one were bred, care would be needed to ensure that increased retention does not become an ecological defect of the plant in the pasture.

The universally low percentage of seed set in *Brachiaria* may have genetic origins associated with polyploidy, or it may equally reflect a physiological limitation in, for example, the capacity to divert assimilate into reproductive activity. Causes of failure thus need to be understood before tackling low seed set.

Seed dormancy is a strong generic characteristic, inconvenient in seed testing and sometimes prejudicial to establishment. Its value for pasture persistence is often inferred, but is essentially unknown. Selection for weaker dormancy may be possible, but its consequences would be unpredictable. A safer policy would therefore be to persevere with understanding and accommodating to dormancy rather than to change it.

To improve seed production of existing commercial taxa and develop production systems for new cultivars, researchers should involve, *from the earliest stages*, those who grow and know the seed crops, the producers and agronomists, whose initiatives over the last 30 years have contributed substantially to the remarkable success of the genus.

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References

To save space, the following acronyms are used in place of publishers' names:

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

CPAC = Centro de Pesquisa Agropecuária dos Cerrados

CSIRO = Commonwealth Scientific and Industrial Research Organisation

ICA = Instituto Colombiano Agropecuario

INRA = Institut national de la recherche agronomique

IPEAN = Instituto de Pesquisa Agropecuária do Norte

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Animal Science

NZSAP = New Zealand Society of Animal Production

TGSA = Tropical Grasslands Society of Australia

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Chapter 9

Seed Production: Perspective from the Brazilian Private Sector

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Abstract

Brachiaria cultivars developed by forage research programs are delivered to commercial livestock producers through the vehicle of seed. Over the past 15-20 years, a large, dynamic industry has developed in Brazil for the production of *Brachiaria* seed. This paper describes the history of this industry, its magnitude, and projections for the future. The seed production technology that has evolved in Brazil is briefly described. Constraints to the commercial development and exploitation of *Brachiaria*, as perceived from the private sector, are listed. The priorities of the private sector do not always coincide entirely with those of public sector researchers; a plea is therefore made for closer cooperation between private and public sector efforts to develop and exploit these forage grasses to benefit tropical livestock production.

Introduction

Brazil is a large tropical and subtropical country, which occupies about half of the South American continent (8.51 million km^2), but is relatively sparsely populated, with only 19.4 inhabitants per km^2.

Brazil's cattle population is close to 160 million head, raised almost exclusively on grazed pastures covering an estimated 160 million hectares, of which about 40% are sown to introduced species; the remaining 60% are unimproved native pastures.

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The first introduction of *Brachiaria* germplasm for experimental use was during the 1950s, to the Instituto de Pesquisa Agropecuária do Norte (IPEAN) in Belém, Pará State, in the eastern Amazon basin (Argel and Keller-Grein, Ch. 14, this volume; Keller-Grein et al., Ch. 2, this volume). However, large-scale use of signalgrass (*B. decumbens* cv. Basilisk) in Brazil began only in the early 1970s, when commercial quantities of Australian seed were imported.

Before 1970, improved pastures in the Brazilian tropics were sown mainly to *Panicum maximum* (guineagrass) on fertile soils; *Melinis minutiflora* primarily on infertile, sandy soils; and *Hyparrhenia rufa* on heavier, more fertile soils. The remaining 10% of improved tropical pastures were sown to *Cynodon* species (bermudagrass), *Pennisetum* species, and tropical forage legumes (Table 1).

Great expectations were soon raised for *B. decumbens* as a panacea for the infertile soil savannas of central Brazil. However, the limitations of the "miracle grass" soon became apparent with large-scale commercial use. Populations of spittlebugs (Homoptera:Cercopidae), probably stimulated by vast monocultures of the susceptible host, *B. decumbens* cv. Basilisk, periodically devastated large areas of the improved pastures, particularly in more humid environments (Valério et al., Ch. 6, this volume). A hepatic disorder in livestock, associated with grazing signalgrass pastures, was found to cause weight loss and even death, particularly of young animals. The cause of this phenomenon is still not entirely understood (Lascano and Euclides, Ch. 7, this volume). However,

Table 1. Estimated composition of improved pastures in the Brazilian tropics during the early 1970s.

Soil fertility, management system	Predominant species	Area of improved pasture (%)
High, extensive	*Panicum maximum*	20
Medium, extensive	*Hyparrhenia rufa*	30
Low, extensive	*Melinis minutiflora*	40
Variable, intensive	*Cynodon, Pennisetum*, legumes	10

while photosensitization continues to be a problem, it can be reversed by removing affected animals from *B. decumbens* pastures.

It appears that the severity of spittlebugs, which was always a periodic, rather than chronic, threat to pasture productivity, has decreased with time. This may be because ranchers have learned how to better manage *Brachiaria* pastures, to minimize spittlebug damage or even to build up natural control organisms. But the risk of spittlebug attacks still essentially precludes the use of the susceptible cv. Basilisk for pasture development in the humid tropics.

In 1973, Hermógenes Leitão Filho of the Instituto Agronómico de Campinas (São Paulo State) discovered that *B. humidicola* produced viable seed despite strong seed dormancy (H. Leitão Filho, 1973, personal communication). This species was at first viewed as a spittlebug-resistant replacement for *B. decumbens*. Further experience, later confirmed by controlled entomological research, showed that although *B. humidicola* is more tolerant of spittlebug damage than *B. decumbens*, it is an excellent host for the nymph, and when high population levels are reached, severe damage can occur.

Despite the limitations of the early *Brachiaria* cultivars, their use continued to spread, because of their desirable attributes. Probably the primary reason for expanded use of *Brachiaria* species is that they offer scope for greatly increasing the productivity of grazing lands on the infertile, highly acid soils that cover several hundred million hectares in Brazil. They are high-yielding grasses with reasonable to good forage quality. Forage production during the dry season, which is a critical period for animal performance, is far superior to that of forage grasses available previously.

At least a partial solution to the problem of spittlebugs came in 1984, when EMBRAPA released *B. brizantha* cv. Marandu, an introduction with a high level of antibiotic resistance to the insect. Because of this, cv. Marandu began to displace the susceptible cv. Basilisk. Being better adapted to higher fertility soils than either *B. decumbens* or *B. humidicola*, cv. Marandu also began to displace other tropical grasses, such as guineagrass, bermudagrass, and rhodesgrass (*Chloris gayana*), which were traditionally sown on more fertile soils.

By 1994, more than 2 decades after the first commercialization of *B. decumbens* in Brazil, the distribution of tropical forage species had changed dramatically, with nearly 80% of improved pastures sown to one or another *Brachiaria* species (Table 2).

Production Technology

The initial stimulus for Brazilian production of *Brachiaria* seed was the high price (US$10/kg) of imported

Table 2. Estimated composition of improved pastures in the Brazilian tropics during 1994.

Soil fertility, management system	Predominant species	Area of improved pasture (%)
High-medium, extensive	*Brachiaria brizantha* cv. Marandu	45
Medium-low, extensive	*B. decumbens* cv. Basilisk	30
Low, humid, extensive	*B. humidicola*	3
Variable, intensive	*Panicum maximum*,	10
	Andropogon gayanus,	5
	legumes,	5
	B. ruziziensis,	1
	B. dictyoneura cv. Llanero	1

Australian seed containing only 10% by weight of pure live seed. Early attempts to produce *Brachiaria* seed in Brazil were based on practices in Australia established by a commercial seed enterprise (Yates Ltd.) and the Division of Tropical Crops and Pastures belonging to the Commonwealth Scientific and Industrial Research Organisation (CSIRO).

Because standard practice at the time was combine harvest of the standing seed crop, contemporary research was directed at maximizing the yield and quality of combine-harvested seed and overcoming its dormancy. Means were also sought to improve germination and establishment in the field.

Meanwhile, Brazilian farmers were beginning to experiment with collecting shed *Brachiaria* seed from the ground. The resulting product, a mixture of ripe seed, soil, weeds, and other kinds of trash, was sown almost out of desperation, as a "quick and dirty" (and cheap) means of establishing some sort of productive pasture adapted to the extremely infertile, low-value land of the Brazilian Cerrados.

During the 1980s, as the use of signalgrass expanded in central Brazil, it gradually became apparent that the introduction of *Brachiaria* species tolerant of acid soils represented a technology that would radically transform these vast, previously undeveloped savannas.

Indigenously grown *Brachiaria* seed at first steadily replaced imported Australian seed in Brazil; then, during the 1980s, Brazilian seed began to enter external markets in neighboring South American countries, particularly Venezuela, Paraguay, and Bolivia.

For this developing export market, the crude product recovered from the ground was no longer adequate, although early studies had shown that fallen seed recovered from the ground was, in fact, of higher quality (viability and germination) than combine-harvested seed (Hopkinson et al., Ch. 8, this volume). Efforts expended on the special problems of cleaning the extremely dirty seed recovered from the soil led to a product with up to 95% purity and about 90% germination, a significant improvement over direct-harvested seed (Table 3). The shelf-life of fallen seed harvested from the ground is also longer (18-36 months under good warehouse conditions) than that of combine-harvested seed. Except for *B. humidicola*, nearly all Brazilian *Brachiaria* seed is now recovered from the ground.

Table 3. *Brachiaria* seed production in Brazil.

Species	Germination (%) of seed harvested from	
	Plant	Soil
B. brizantha cv. Marandu	20-30	70-80
B. decumbens cv. Basilisk	30-50	75-85
B. humidicola	40-70	nil
B. ruziziensis	50-70	70-80

SOURCE: L. F. Santos Filho, unpublished data.

Processing Technology and Quality Control

Processing of *Brachiaria* seed begins directly in the field, with a crude screening to remove soil and other trash. Conventional machinery for cleaning crop seed has been adapted for the job of cleaning *Brachiaria* seed.

Seed is received from the field and paid for, based on a tetrazolium test of viability, a test not generally used for other forage seed. Routine germination tests are conducted, taking into account the special problems of *Brachiaria* seed dormancy, before seed is marketed.

The quality of commercially marketed seed is expressed in terms of pure live seed (PLS), which is the product of the purity of the seed lot (weight of pure seed as a proportion of total weight, including nonseed trash and inert material) and percentage of germination. Thus, a seed lot that has 90% pure seed and 80% germination has a PLS rating of 72%. Planting rate in kg/ha of any seed lot can be calculated by dividing the standard planting rate of 240 PLS "points"/ha by the PLS rating of the particular lot of seed. Thus, if a seed lot has a PLS rating of 24% (e.g., 60% purity and 40% germination), the seeding rate would have to be 10 kg/ha; if it has a PLS rating of 80% (e.g., 95% purity and 84% germination), seeding rate would need only be 3 kg/ha.

Market Volume

The *Brachiaria* seed industry in Brazil has grown to meet the large internal demand and an expanding export market. The volume and value of commercial *Brachiaria* seed is truly astonishing, placing it in competition, in monetary value, with major cereal crops (Table 4).

Table 4 summarizes the Brazilian internal market for *Brachiaria* seed, expressed on the common basis of PLS points (kg of seed multiplied by the variable percentage of pure live seed), where a standard seeding rate is 240 PLS points/ha; that is, 2.4 kg seed of 100% PLS or 10 kg of seed of 24% PLS. Even assuming that only 50% of *Brachiaria* seed is marketed through recognized commercial channels, the internal Brazilian market for this commodity is on the order of 30,000 t, with a market value of more than US$100 million annually.

Current exports of *Brachiaria* seed from Brazil are estimated at only about 10% of the internal Brazilian market. However, this incipient export market is seen as growing, with the full potential only beginning to be met.

Seed export requires study of the particular market demands and quarantine requirements of each national market. Colombia, for instance, requires acid-scarified seed with 90%-95% purity and 80%-85% germination (*B. decumbens*)

Table 4. The commercial market for *Brachiaria* seed in Brazil.

Item	Amount
Total pasture area (ha)	160,000,000
Native pastures 40% (ha)	64,000,000
Improved pastures (60%)	96,000,000
Pasture renewal/year (10%) (ha)	9,600,000
Use of *Brachiaria* (80%) (ha)	7,680,000
PLS points[a]/ha needed (no.)	240
Total PLS points/year (no.)	1,843,200,000
50% sold by seed companies (no.) unit	921,600,000
Value per unit (US$/PLS)	0.125
Estimated market value (US$)	115,200,000

a. PLS points = % pure live seed, e.g., 8 kg of seed with 30% pure live seed are the equivalent of 240 PLS points.

or 90% purity and 60% germination (*B. humidicola*). The requirement for acid scarification was originally thought to guarantee freedom from the aftosa (foot-and-mouth disease) virus. However, this import requirement appears to have no biological basis, as the virus is short-lived in the absence of a bovine host, and simply spelling *Brachiaria* pastures prior to seed harvest is sufficient to ensure aftosa-free seed. The quarantine rules, however, remain in effect, unnecessarily complicating seed marketing.

Other countries import seed of much lower PLS content (e.g., 40%-70%), which is therefore ready to plant without local admixture with an inert carrier material.

Demand for seed quality is not uniform over markets. While high-quality seed (i.e., purity up to 95% and germination about 80%) can be produced, this comes at a cost. Further, it is not always practical to sow a small quantity (say 3 kg) of high-quality seed uniformly over a hectare. As hand-broadcasting *Brachiaria* seed is a common practice in Brazil, sowing is often easier, more uniform, and less risky when a product of lower quality but higher volume is used (e.g., 10 kg/ha of seed of 24% PLS). But if seed is to be used far from production sites, the preference for planting material of higher volume but lower quality is tempered by the higher transportation costs involved, compared with a higher quality product.

Potential Export Markets for Brazilian *Brachiaria* Seed

Most Central American countries, Mexico, and the Caribbean islands are only beginning to establish large areas of *Brachiaria* pastures. Mexico, in particular, represents an attractive potential market. The strength and aggressiveness of the Brazilian seed sector is demonstrated by some enterprises (e.g., NATERRA) studying even such nontraditional markets as southern USA, which has traditionally been serviced locally, and certain Asian countries, which have traditionally been served either by small-scale local seed production or by Australian commercial seed producers.

Constraints

Private sector participants in pasture improvement see several constraints to the further development of *Brachiaria*

species as commercial forage grasses. Research programs should consider attributes that would be desirable in new cultivars:

1. Palatability to horses, which do not consume *B. decumbens*.
2. Adaptation to high-altitude, low-temperature environments in the tropics.
3. Adaptation to subtropical environments with greater seasonal variation, particularly of temperature and precipitation.
4. Adaptation to lower rainfall areas.
5. Adaptation to shaded conditions, such as under plantation crops.
6. More uniform distribution of dry matter forage production throughout the year.
7. Freedom from toxins that cause photosensitization.

Research is urgently required on the following topics:

1. Practical means of reliably overcoming postharvest dormancy in *B. humidicola* and *B. dictyoneura*[1] cv. Llanero.
2. Clarification of the threat of aftosa contamination from *Brachiaria* seed and modification of quarantine requirements for imported seed in accordance with biological reality.
3. Seed longevity, particularly the effect of scarification practices and storage conditions on shelf life of commercial seed.

Collaboration between Public and Private Sectors

The process of formal release of new forage cultivars in Brazil is essentially a public sector activity, although "informal releases" are not uncommon. The process is likely to become more productive and efficient with active participation from the private sector. Mechanisms should be sought to achieve this collaboration between the two sectors.

Collaboration between the public and private sectors is also required in the area of quarantine and other restrictions on the free movement of forage seed in international commerce. Uniform legislation among tropical American countries would greatly enhance the movement of seed across international boundaries; this would make seed more easily available, thus enhancing adoption rates of new cultivars.

The private seed sector has special interests that are not entirely compatible with those of public sector researchers or quarantine officers. Mechanisms should be sought for collaborative activity, to enhance the commercial exploitation of *Brachiaria* cultivars for the benefit of national livestock industries and, ultimately, the consumers of livestock products.

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Chapter 10

Genetics, Cytogenetics, and Reproductive Biology of *Brachiaria*

C. B. do Valle* and Y. H. Savidan**

Abstract

Two essentials for breeding new cultivars of *Brachiaria* are germplasm diversity and information on basic biological aspects of major species. This paper reviews current knowledge on the cytological behavior, mode of reproduction and its inheritance, and crossing compatibility of different species. The two of major agronomic importance—*B. decumbens* and *B. brizantha*—are tetraploid (2n = 4x = 36) and apomictic, that is, the embryo is produced without fusion of male and female gametes. Apomixis, although not common, is found throughout the plant kingdom and is often associated with polyploidy. Hence, it is frequently accompanied by meiotic anomalies leading to reduced pollen fertility. Sexuality has been found at the diploid level in these species and in *B. ruziziensis*, and is generally associated with regular chromosome pairing and division. As a breeding tool, apomixis offers several advantages, because it associates fixation of hybrid vigor with seed propagation. Apomictic hybrids breed true, and superior genotypes can be rapidly increased by seed. The discovery of completely sexual plants in cross-compatible species of *Brachiaria* and the development of practical clearing techniques for the observation of ovules prompted studies of inheritance of apomixis. Results suggest a simple, monogenic control of mode of reproduction, with apomixis dominant over sexuality. These investigations open up promising new possibilities for manipulating apomixis in breeding programs.

Introduction

The genus *Brachiaria* encompasses about 100 species with wide morphological and phenological differences (Keller-Grein et al., Ch. 2, this volume; Renvoize et al., Ch. 1, this volume). However, only a few varieties adapted to infertile and acid soils are grown extensively in cultivated pastures in tropical America (Argel and Keller-Grein, Ch. 14, this volume; Pizarro et al., Ch. 15, this volume). The risk to these extensive monocultures is obvious, and new varieties of *Brachiaria* are urgently needed. These can be developed either by selecting superior genotypes from the natural diversity or by hybridizing to obtain novel genetic combinations (Miles and Valle, Ch. 11, this volume). Either way, an adequate germplasm base is essential. Also essential to a successful breeding program is knowledge of basic characteristics, such as mode of reproduction, chromosome behavior, and ploidy levels within and among compatible species.

In several families of angiosperms, sexual reproduction (*amphimixis*) is replaced by or combined with asexual reproduction, or *apomixis*—a word derived from the Greek, meaning "without mixing"—where an embryo is preduced without the fusion of male and female gametes. The offspring resulting from apomictic reproduction of a single plant is therefore a true clone. In its strict sense,

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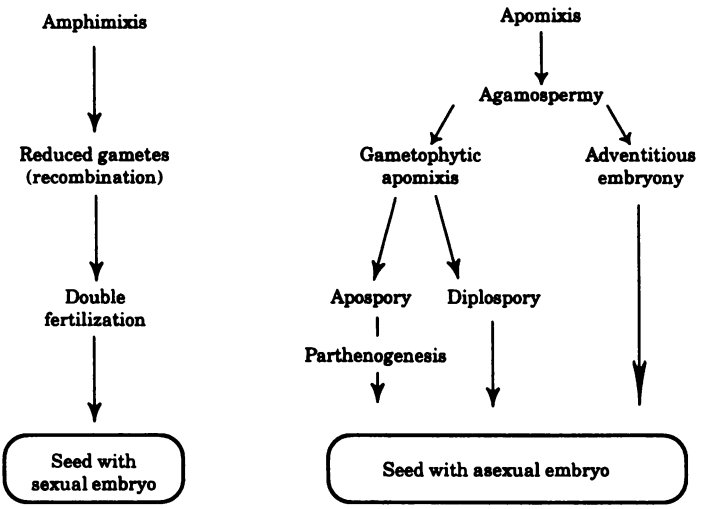

Figure 1. Embryo formation in plants of different modes of reproduction.

apomixis has come to signify the formation of an asexual embryo inside a gametophyte (Figure 1). Some useful terms in the study of apomicts are defined here:

Agamospermy: asexual reproduction by means of seeds.

Adventitious embryony: production of somatic embryos directly in the ovules of the meiotic mother sporophyte, in the form of nucellar or integumental outgrowths.

Diplospory: production of an unreduced gametophyte directly or indirectly from a megaspore mother cell.

Apospory: production of an unreduced gametophyte directly from a somatic cell of the nucellus or chalaza. The gametophyte (embryo sac) of the diplosporous and aposporous types generally includes an egg cell, besides other nuclei.

Agamic complex: species in a genus that are partitioned into diploid and sexual species on the one hand, and polyploid and apomictic on the other. Genetic recombination is possible within the agamic complex, by crosses with intermediate or compatible species. In these complexes in which apomixis, hybridization, polyploidization, haploidization, and sexuality operate, the variation observed is often continuous, and species identification can become difficult.

Parthenogenesis: development of the egg cell into an embryo without fertilization.

Pseudogamy: seed development requiring pollination of polar nuclei even without fertilization of the egg cell.

Facultative apomict: plant that produces both maternal progeny by apomixis and other offspring by the normal sexual process. This can occur because the aposporic embryo sac in certain ovules either does not develop at all or develops slowly enough to allow the haploid embryo sac derived from the megaspore to be fertilized and reach maturity.

Obligate apomict: plant that produces only maternal progeny. Most apomicts were classified as obligate in the past, because of the limitations of the tools and methods available for screening mode of reproduction; that is,

morphological progeny tests or paraffin sectioning of a limited number of ovaries per plant.

Asker and Jerling (1992) question whether obligate apomicts really exist, since most plants will show some residual sexuality at the cytological level if enough ovaries are examined. Even if certain biotypes do not produce meiotic embryo sacs, the species as a whole is hardly ever found to be obligately apomictic.

As a breeding tool, apomixis offers several advantages: it is the only mode of reproduction that associates fixation of hybrid vigor with seed propagation. Apomictic hybrids breed true, and superior genotypes can be rapidly increased by seed. Apomixis also simplifies commercial hybrid seed production, because isolation is not necessary, parental lines need not be increased, mechanical mixture is less likely, and outcross contamination does not occur. The number of highly trained production personnel, and thus seed production costs, can be reduced. The important adaptive advantage of apomixis is that it restores full fertility in plants that would otherwise be sterile because of chromosomal abnormalities.

Apomixis, although not common, is found in diverse and unrelated plant families of the plant kingdom. Reviews by Brown and Emery (1958), Gustafsson (1947), and Nygren (1967) report apomixis in over 30 families, including more than 300 species of higher plants. Quarin (1992) reviewed 58 species from the genus *Paspalum* and classified 37 as apomicts. Extrapolating to the 400 species in this genus alone, perhaps more than 250 species of *Paspalum* are apomictic. More than 500 species in the most important genera of the Panicoideae subfamily are estimated to exhibit apomixis. Apomictic reproduction also occurs in species related to important crop plants, as well as in many perennial forage grasses. Investigations of the cytological and genetic basis of apomixis and the discovery of sexuality in species previously considered obligate apomicts open up promising possibilities for manipulating apomixis in breeding programs.

Cytogenetics of *Brachiaria*

Cultivars of *Brachiaria* have gained commercial importance in the last 30 years. But despite their widespread use and the economic impact they have caused, little is known about the biology of these grasses. Darlington and Wylie (1955) determined the basic chromosome numbers for the genus to be x = 9 or x = 7. Other reports on chromosome numbers of *Brachiaria* (Goldblatt, 1981; 1984; Moffet and Hurcombe, 1949; Moore, 1970) are summarized in Table 1. Valle et al. (1987) have described pachytene chromosomes of *B. ruziziensis*, and an ideogram has been proposed.

Natural diploids of *B. brizantha*, *B. decumbens*, and *B. ruziziensis* exhibit regular meiosis, with normal chromosome pairing as 9 bivalents. Their tetraploid counterparts, however, display irregular meiosis, with univalents and quadrivalents being formed. Tetraploids of *B. ruziziensis* were artificially induced by colchicine treatment (Swenne et al., 1981). Sotomayor-Rios et al. (1960) reported irregular meiosis, with laggards in 69% of cells of tetraploid *B. brizantha*. In that instance, only 16% of spore quartets appeared normal, and 14% of pollen stained completely. Pritchard (1967) reported irregular meiosis in pollen mother cells of tetraploid *B. decumbens*, with the presence of laggards, uni-, tri-, and quadrivalents. Of the mature pollen grains observed, 70% were empty or incompletely developed. One tetraploid accession of *B. humidicola* was found to pair regularly as 18 bivalents in meiosis (Valle and Glienke, 1991) and to reproduce sexually. Other tetraploid and hexaploid apomictic accessions of this species have been examined and display irregular meiosis (Valle, 1986; C. B. do Valle, unpublished data).

Brachiaria mutica and *B. arrecta* (syn. *B. radicans*) are tetraploid species,

Table 1. Chromosome numbers for some *Brachiaria* species of agronomic importance as forages.

Species	Chromosome no.	Reference
B. arrecta	2n = 4x = 36	Schank and Sotomayor-Rios, 1968
B. brizantha	2n = 2x = 18	Carnahan and Hill, 1961 Valle and Glienke, 1991
	2n = 4x = 36	Nath and Swaminathan, 1957 Sotomayor-Rios et al., 1960 Carnahan and Hill, 1961 Nassar, 1977 Ndikumana, 1985 Valle, 1986 Basappa et al., 1987
	2n = 6x = 54	Carnahan and Hill, 1961
B. decumbens	2n = 2x = 18	Valle et al., 1989 Valle and Glienke, 1991
	2n = 4x = 36	Zerpa, 1952 Pritchard, 1967 Nath et al., 1970 Nassar, 1977 Basappa and Muniyamma, 1981 Ndikumana, 1985 Valle, 1986
B. dictyoneura	2n = 6x = 42 n = 7	Carnahan and Hill, 1961 Moffet and Hurcombe, 1949
	2n = 6x = 54[a]	Valle, 1986
B. humidicola	2n = 4x = 36	Valle and Glienke, 1991
	2n = 6x = 54	Valle, 1986
B. jubata	2n = 4x = 36	Goldblatt, 1981 Valle, 1986
B. mutica	2n = 4x = 36	Warmke, 1951 Nath and Swaminathan, 1957 Nassar, 1977 Basappa and Muniyamma, 1981
B. ruziziensis	2n = 2x = 18	Schank and Sotomayor-Rios, 1968 Ferguson, 1974 Ferguson and Crowder, 1974 Ndikumana, 1985 Valle, 1986 Valle et al., 1987

a. The accessions studied may have been *B. humidicola* and not *B. dictyoneura*.

the first with irregular chromosome pairing and apomictic reproduction; the second with reasonably regular bivalent pairing and sexual reproduction. A natural hybrid between these species was discovered and shown to be completely sterile (Souto, 1978). Evidence points to the association of apomixis with polyploidy and irregular meiosis on the one hand, and sexuality and regular chromosome pairing on the other, as has been discussed for other genera, for example, *Paspalum* (Quarin, 1992) and the *Bothriochloa* agamic complex (deWet and Stalker, 1974).

The germplasm collection assembled at CIAT (Keller-Grein et al., Ch. 2, this volume), in collaboration with other international and national organizations in Africa, includes several other species of *Brachiaria*, some with good potential for use directly as pasture plants and in breeding programs. Extensive analyses of

chromosome number and behavior are still to be done, but should help identify species and accessions worth incorporating into phylogenetic studies.

Reproductive Biology

The cytological path taken in the formation of the embryo sac—megasporogenesis—will determine the mode of reproduction and the nature of the resulting progeny. On the male side, microsporogenesis may determine fertility, and therefore the pollen contribution to the genetic makeup of the resulting progenies.

Apomixis is generally associated with polyploidy; hence, it is frequently associated with meiotic anomalies leading to reduced pollen fertility (reports by several authors, reviewed by Ndikumana, 1985).

Gobbe et al. (1982) studied male and female embryogenesis in detail in diploid and artificially induced tetraploid *B. ruziziensis*. This study used microsporogenesis and microgametogenesis as a reference scale for the comparison of events in megasporogenesis and megagametogenesis. Male meiosis takes place early, while the archespore waits to begin meiosis until dyads and tetrads are already formed in the anthers. The female meiotic divisions are considerably slower on the induced tetraploid (4x) plants than on natural diploids (2x). Only when the pollen grain becomes binucleate do the 2x and 4x female gametophytes complete their development. Maturation of the megagametophyte proceeds much faster in the tetraploids than in the diploids; therefore, both megagametocytes (2x and 4x) are ready for fertilization at approximately the same time. Further maturation proceeds at similar rates in diploids and tetraploids. Other differences observed have been on nucellar cells, which are multinucleate and numerous in the tetraploids, and binucleate and fewer in the diploids. Also, the tetraploid microsporocyte nucleus often contains two nucleoli, while the diploid microsporocyte contains only one.

Ndikumana (1985) compared sexual with aposporic development inside the embryo sacs of one ecotype of *B. brizantha* and one of *B. decumbens* from Burundi. The apomictic materials from both species showed similar development of embryo sacs, the aposporic sacs attaining mature stages earlier than the meiotic sacs. This fact can be of paramount importance in determining the next step—fertilization or parthenogenesis—and therefore the effective reproductive behavior of the plant. Both accessions behaved as facultative apomicts in this study, with several gametophytes per ovule. Often, sexual and aposporic (single and multiple) sacs were observed sharing the same ovule. The corresponding stages in male and female gametogenesis are described in Table 2. Despite small differences,

Table 2. Stages of development in female and male gametogenesis of greenhouse-grown *Brachiaria brizantha* and *B. decumbens* plants.

Female		Male
Sexual	Aposporic	
Archespore	Hypertrophiated cells vacuolated	Microspore not vacuolated
Tetrad	Hypertrophiated cells vacuolated	Microspore vacuolated
Embryo sac	Embryo sac	Microspore vacuolated
2-nucleate	2-nucleate	First mitosis
4-nucleate	4-nucleate maturing	First mitosis
8-nucleate	4-nucleate mature	First mitosis
Maturing	Mature	2-nucleate pollen grain
Mature	Mature	3-nucleate pollen grain

SOURCE: Ndikumana, 1985.

male gametogenesis may be used to estimate stages of female gametogenesis in the same flower for both species.

Megagametogenesis may follow two pathways in *Brachiaria* (Figure 2). The first is the sexual, where regular meiosis of the megaspore mother cell results in a tetrad of reduced cells. One of these (chalazal surviving megaspore) undergoes three mitoses, resulting in a *Polygonum*-type reduced embryo sac. Its nucleoli differentiate into one egg cell, two short-lived synergids, two polar nuclei, and three antipodal cells. The second pathway is the asexual, where the aposporic embryo sacs develop from enlarged, unreduced nucellar cells when all four megaspores degenerate. Nucellar cells undergo two mitoses, producing 4-nucleate (one egg cell, two short-lived synergids, and one polar nucleus), *Panicum*-type embryo sacs.

Mode of reproduction has been determined for a large germplasm collection of *Brachiaria*, with the objectives of finding sexually compatible species for breeding purposes and of establishing a germplasm conservation strategy (Valle, 1990; Valle and Miles, 1992; 1994). Embryo-sac structures were examined, using clearing with methyl salicylate and interference contrast microscopy according to Young et al. (1979); Table 3 summarizes the results. Sexuality was found in accessions of species previously believed to contain only apomicts (*B. decumbens*, *B. humidicola*, *B. dictyoneura*, *B. brizantha*). Some species had no prior report on mode of reproduction: *B. serrata*, *B. platynota*, and *B. subulifolia* (Valle, 1990).

Chromosome counts were taken on microsporocytes of various sexual accessions, using traditional acetocarmin

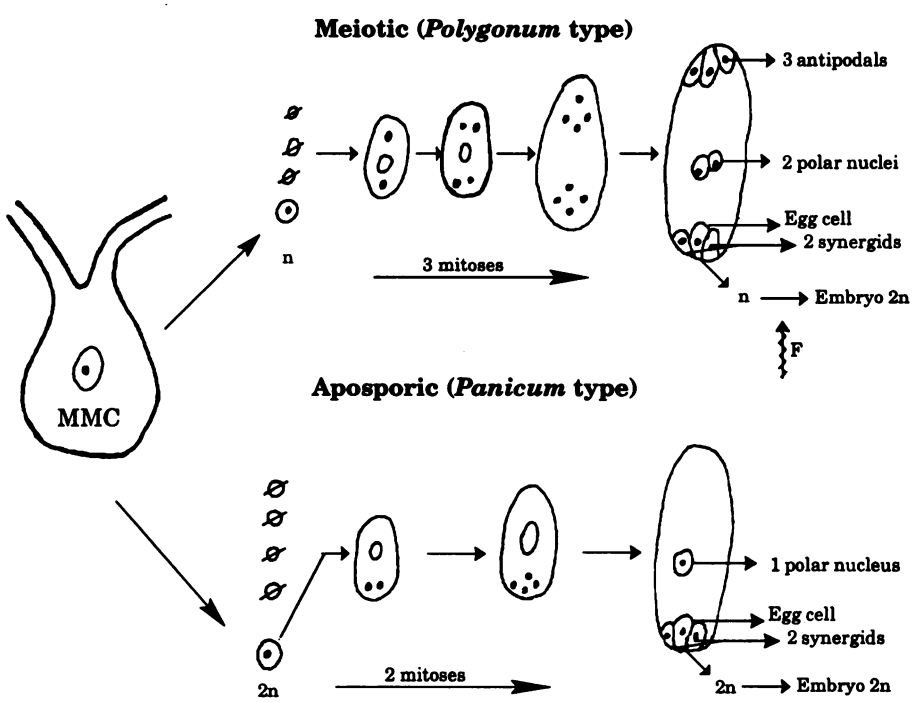

Figure 2. Meiotic and aposporic embryo sac formation in sexual and apomictic plants of *Brachiaria*. (MMC = megaspore mother cell; F = fertilization.)

Table 3. Mode of reproduction of 17 species of *Brachiaria*, based on embryo-sac analysis.

Species[a]	Accessions evaluated (no.)	Reproductive mode		
		Sexual (no.)[b]	Apomictic[c]	
			(no.)	Range of sexuality (%)
B. adspersa	1	1	0	-
B. arrecta	4	4	0	-
B. bovonei	4	0	4	7-14
B. brizantha	275	1	274	0-74
B. comata (syn. *B. kotschyana*)	1	1	0	-
B. decumbens	65	23	42	3-56
B. deflexa	1	1	0	-
B. dictyoneura	6	1	5	0-43
B. dura	1	1	0	-
B. humidicola	60	3	57	3-66
B. jubata	41	6	35	0-47
B. nigropedata	2	0	2	5-11
B. platynota	4	3	1	61
B. ruziziensis	36	36	0	-
B. serrata	2	2	0	-
B. subquadripara (syn. *B. miliiformis*)	2	2	0	-
B. subulifolia	5	0	5	9-38
Total	510	85	425	

a. Taking into account corrections in species determinations by S. A. Renvoize (1993, unpublished report).

b. Aposporic sacs were never observed.

c. Range of sexuality (percentage of meiotic sacs) observed in apomictic accessions.

SOURCES: Modified after Valle, 1990; Valle and Glienke, 1991; and C. B. do Valle, B. L. Maass, M. L. Escandón, and L. A. Ortega, unpublished data.

squashes. The one sexual *B. brizantha* and all sexual *B. decumbens* were determined to be diploids with regular bivalent pairing. The sexual *B. humidicola* accession is tetraploid, with regular bivalent pairing during meiosis. The tediousness of making chromosome counts has prevented further studies with this germplasm. Flow cytometry may be used in the near future to establish ploidy levels, aiding selection of material for phylogenetic studies and breeding.

Genetic Control of Apomixis

Since the first crosses made by Mendel on *Hieracium*, more than 100 years ago, much has been written on the genetic control of apomixis and its potential uses in breeding.

An early hypothesis assumed several genes were involved based on the logic that apomixis, like any mode of reproduction, is a complex physiological process. But this hypothesis of several genes is weakened, to some extent, by the success of apomixis across plant species, genera, and families. In fact, if several genes are involved in the different steps of the developmental pathway, any single mutation or recombination can produce a plant capable of one step but not the others, condemning it to sterility.

The potential for breeding an apomictic species can be fully realized only if the apomictic mechanism involved is understood and the genetics of gametophytic apomixis determined. Bashaw (1980) pointed out that apomictic species have been poor subjects for genetic

studies because most crosses had been made with facultative apomicts, leading to ambiguous results.

The discovery of completely sexual biotypes in species of tropical and subtropical apomictic forage grasses allowed better hypotheses to be developed. These materials proved especially suitable, because intraspecific and/or interspecific hybridization became possible (Miles and Valle, Ch. 11, this volume). Many hybrids were produced, and mode of reproduction could be determined, using either progeny tests or newly available and efficient techniques for observing ovules. Another asset is the fact that the aposporous plants of the *Panicum* type, which produce a 4-nucleate sac(s) per ovule, can be easily differentiated from the sexually reproducing plants, which display a solitary 8-nucleate sac (Figure 2).

In contrast with the early hypothesis, a simple genetic determinism (mono- or oligogenic) was proposed for some grasses of the tribes Paniceae and Andropogoneae (Harlan et al., 1964; Ndikumana, 1985; Savidan, 1983; Taliaferro and Bashaw, 1966). Harlan et al. (1964) stated that apomixis was dominant, but not an allelic alternative to sexuality in the *Bothriochloa-Dichanthium* complex. The first genetic analysis that used clearing in an aposporous species was conducted on *Panicum maximum* (Savidan, 1978; 1982). The results demonstrated that apospory was transmitted from one generation to the next by a single dominant gene, in contrast with other studies, which had stated that two genes were involved (Taliaferro and Bashaw, 1966). One of these studies was based on *P. maximum* (Hanna et al., 1973).

Savidan (1982) closely observed apomictic and sexual hybrids of *P. maximum* at the same stage of floral development. Aposporous embryo sacs matured much earlier than the meiotic sacs. This strongly suggested that failure of fertilization could simply be a structural (or physiological) consequence of the first event—the replacement of the reproductive cell by a somatic cell—and not the expression of a second genic difference. This again was subject to controversy, prompting reexamination of existing data, taking into account the timing differences between sexual and apomictic processes.

According to Nogler (1984; G. A. Nogler, 1994, personal communication), there are no indisputable data in the literature to reject either the single dominant gene model or the hypothesis of a primary "switch" that induces a cascade of events, such as failure of fertilization, followed by parthenogenetic development of the embryo. A recent analysis of *Cenchrus ciliaris*, where a two-gene model had previously been proposed, presents data that fit the model of one dominant gene (Sherwood et al., 1994). Another recent analysis of *Brachiaria* by Valle et al. (1994) also endorses the one-dominant-gene model. Table 4 summarizes the differences in the origin of the sexual

Table 4. Comparison of seven genetic analyses made on aposporous plant species.

Species	Sexual origin	Screening technique	Cross combinations (no.)	Reference
Bothriochloa-Dichanthium	Diploid	Squash	3[a]	Harlan et al., 1964
Brachiaria species	Diploid	Clearing	10[a]	Valle et al., 1994
Cenchrus ciliaris	Off-type	Progeny test	2[b]	Taliaferro and Bashaw, 1966
C. ciliaris	Hybrid	Clearing	4[a]	Sherwood et al., 1994
Panicum maximum	Off-type	Sectioning	2[b]	Hanna et al., 1973
P. maximum	Diploid	Clearing	12[a]	Savidan, 1982
Ranunculus auricomus	Diploid	Clearing	9[a]	Nogler, 1984

a. Data fit the single-dominant-gene model.

b. Data suggest a two-gene model.

materials and in the techniques used in several genetic analyses, which can account for the differences in interpretations.

More information is needed on the "apomixis gene" and its possible effect, since a single gene can hardly explain (1) the simple segregations observed in sexual x apomictic crossings and, at the same time, (2) the presence of partial expression of the trait (facultative apomixis), and (3) the fact that apomixis is not expressed in diploids. Discrepancies found in the few genera studied have not been fully documented. When apomixis is expressed, as in *B. decumbens* and *B. brizantha*, hybridization with sexual forms produces simple segregation ratios, as will be discussed next.

The failure of early hybridization attempts in *Brachiaria* indicated the need for ploidy compatibility to produce hybrids (Ferguson and Crowder, 1974). Diploid x tetraploid crosses in *B. decumbens* yielded a single, sterile, triploid hybrid (Hacker, 1988). In Belgium, a natural sexual diploid, *B. ruziziensis*, was rendered tetraploid with colchicine (Gobbe et al., 1981; Swenne et al., 1981), and breeding schemes were proposed (Gobbe et al., 1983). In Brazil (CNPGC/EMBRAPA), hybridization was undertaken to determine the inheritance of apomixis and thus manipulate it to develop new, improved hybrids (Valle and Miles, 1992; 1994; Valle et al., 1991; 1993).

Crosses were made, using sexual tetraploid clones of *B. ruziziensis* (ruzi) derived from the original Belgian materials and two natural tetraploid apomicts: *B. brizantha* cv. Marandu (bri) and *B. decumbens* cv. Basilisk (dec) (Figure 3). Sexual plants, selected for good phenotypic characteristics in the field, were hybridized

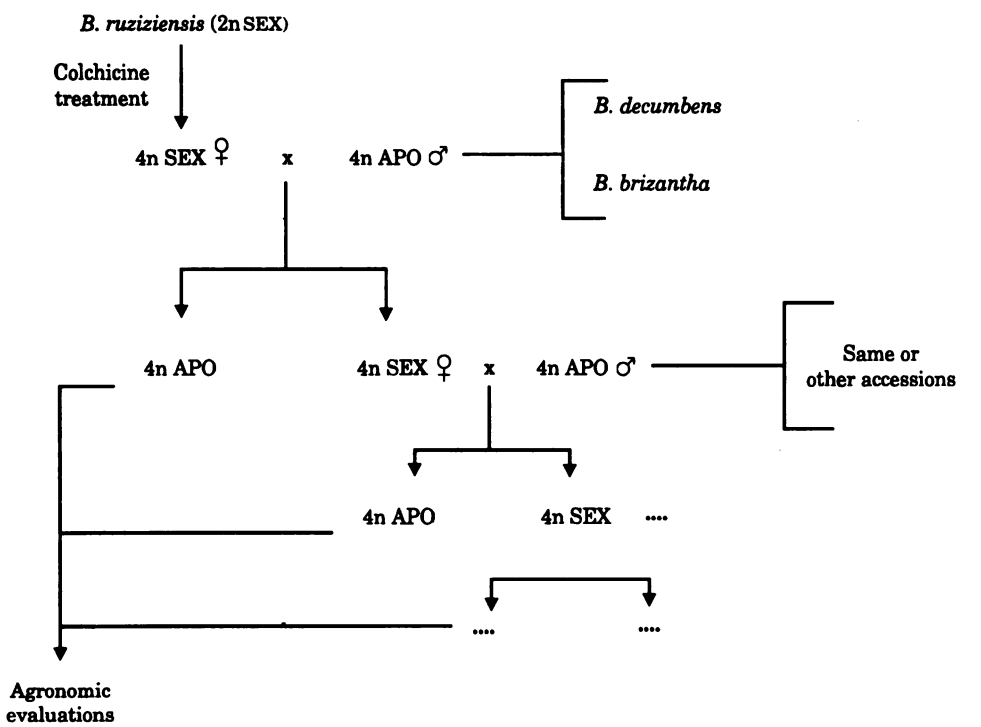

Figure 3. Hybridization scheme for breeding *Brachiaria* (adapted from Gobbe et al., 1983). (APO = apomictic; SEX = sexual.)

in the greenhouse. Pollen from freshly cut inflorescences of the apomicts was collected in petri dishes. Maternal parents were not emasculated, since self-sterility had been reported for these sexual tetraploid clones (Ngendahayo, 1988). To determine mode of reproduction of hybrids, embryo sacs were examined, using methyl salicylate for clearing and interference contrast microscopy according to Young et al. (1979). Because no reliable genetic marker is available to determine the hybrid nature of the progeny, morphological and phenological characters and, in some cases, electrophoresis according to Cruz et al. (1989), were used.

First-generation hybrids resulted in a proportion of sexual to apomictic progeny close to 1:1. There always seemed to be an excess of sexuals, but this could have been because of accidental selfing, since no emasculation was performed. Also, some self-compatibility was detected in at least one clone of *B. ruziziensis*, the progeny of which was not considered for combining results. Sexual and apomictic hybrids were selected for second-generation crosses.

Table 5 summarizes results on segregation for mode of reproduction. Figure 4 shows types of crosses performed to determine inheritance of apomixis in *Brachiaria*. All selfed sexual tetraploid plants, including the original sexual materials and the sexual hybrids, yielded only sexual progeny. Crosses between sexual and apomictic plants gave sexual and apomictic progenies, approximating a 1:1 proportion. Crosses between sexual plants, either at the tetraploid or diploid level, yielded only sexual progeny, indicating recessiveness of sexuality. *Brachiaria ruziziensis* is a cross-pollinating species, therefore, selfing caused abortion of flowers and empty florets, explaining why only 34 viable plants were obtained after hundreds of crosses. First-generation hybrids (125 ruzi x dec; 227 ruzi x bri) were highly polymorphic, and several were selected for their excellent vigor and leafiness.

Segregation in the second-generation hybrids also fit a single-gene model for inheritance of apomixis in *Brachiaria*. Similarly, as reported for *P. maximum* (Savidan, 1983), crosses between facultative apomicts and obligate apomicts resulted in a larger number of apomicts than sexuals. However, the small numbers of viable progenies obtained do not allow conclusive statements. More of these crosses have been carried out, and await analysis to confirm segregation rates (C. B. do Valle and J. W. Miles, unpublished data).

Although this analysis is still in progress, evidence to date points to apomixis being dominant over sexuality.

Table 5. Segregation for mode of reproduction (SEXual or APOmictic) in different types of crosses of *Brachiaria*.

Crosses[a]	Number of plants observed			Expected ratio	Chi²[b]
	SEX	APO	Total		
1. S_1 selfed	22	0	22	1:0	
2. F_1 hybrids	187	165	352	1:1	1.367
3. F_2	12	0	12	1:0	
4. F_1 SEX backcross	22	24	46	1:1	0.044
5. Full-sib mating	64	59	123	1:1	0.113
6. Half-sib mating	81	83	164	1:1	0.012
7. Three-way hybrid	58	42	100	1:1	2.54
8. APO x APO	4	6	10	1:3	
9. SEX x SEX (4x)	7	0	7	1:0	
10. SEX x SEX (2x)	28	0	28	1:0	

a. S_1 = ruzi clones. For explanation of crosses refer to Figure 4.

b. Chi² values greater than 3.84 and 6.63 for significance at 5% and 1%.

SOURCES: Valle and Miles, 1994; Valle et al., 1994.

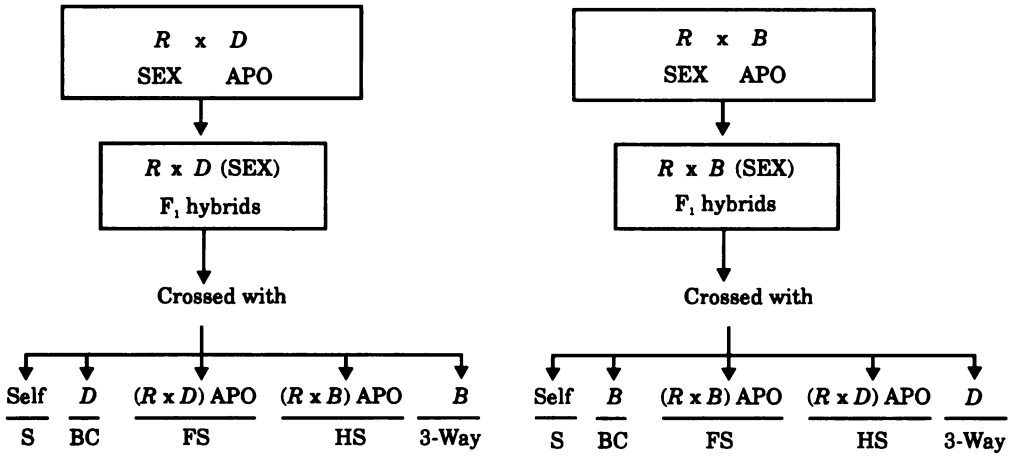

Figure 4. Types of crosses performed to determine inheritance of apomixis in *Brachiaria* (S = F_2; BC = backcross; FS = full-sib mating; HS = half-sib mating; 3-way = three-way cross; *R* = *B. ruziziensis*; *D* = *B. decumbens*; *B* = *B. brizantha*). The data are presented in Table 5.

The proposed genotypes are aa for sexual diploids, aaaa for induced autotetraploids, and Aaaa for apomictic tetraploids, as presented by Savidan (1983) for *P. maximum*. Hybridization of obligate apomicts with sexual plants thus affords the opportunity to produce new gene combinations and permanently fix superior heterozygous progenies for immediate evaluation as potential new apomictic cultivars. Superior sexual genotypes can be integrated into the sexual genetic pool to be used in further crossings.

Chromosome Analysis and Assessment of Reproductive Mode

Determination of chromosome numbers and behavior

Plants with small chromosomes, such as *Brachiaria*, require fixation in propionic rather than acetic acid for better results (Swaminathan et al., 1954). During meiosis, chromosomes are larger than during mitosis, and are present in only half the numbers; therefore, meiosis in actively dividing microsporocytes should be preferred to mitosis in root tips, if flowering occurs freely. Meiosis, however, may exhibit more abnormalities than mitosis, sometimes complicating the interpretation of results. Traditional propiono- or acetocarmin squashes are still the most widely used techniques for simple determination of chromosome number and pairing. More sophisticated techniques are becoming available, such as flow cytometry to estimate DNA quantities and chromosome painting techniques to help identify contrasting genomes. Flow cytometry has enabled more efficient screening of ploidy levels in large numbers of progenies in the maize x *Tripsacum* breeding program of ORSTOM-CIMMYT (Leblanc et al., 1994). This technique could also be useful in the study of the large *Brachiaria* germplasm collection and of the intra- and interspecific hybrids being produced in ongoing breeding programs.

Determination of mode of reproduction

Traditionally, the reproductive mode of a plant was inferred by relative uniformity versus heterogeneity of open-pollinated progeny. These progeny tests were usually based on small

numbers of plants, often grown in conditions unfavorable to the survival of off-types; therefore, erroneous interpretations were probably common. Sexuality expressed at the embryological level does not necessarily result in equivalent proportions of off-types, as discussed earlier (Miles and Valle, 1991).

Another means of determining mode of reproduction is to study ovule structure, using microscopic techniques. Although serial sectioning and coloring provide excellent material for studying megagametogenesis and detecting apomixis, the method is prohibitively tedious for screening large germplasm collections or hybrid populations. New clearing techniques (Crane and Carman, 1987; Herr, 1971; Young et al., 1979) have allowed more efficient and accurate study of apomixis. These techniques require fixation of flowers or floral parts with Carnoy (6:3:1 ethanol, chloroform, and acetic acid), FPA (formalin, propionic acid, and ethanol), or FAA (formalin, acetic acid, and ethanol); dissection of ovaries; and clearing and mounting of ovaries on microscope slides in clearing fluid for examination. Phase or interference contrast microscopy may be used. Interpretation of observed structures requires training and considerable experience. Although these techniques allow screening of large numbers of plants, they are still tedious, and consistency of results depends on several factors, such as age of flowers, care in extraction and clearing of ovaries, and expertise in identifying structures.

Cruz et al. (1989) used electrophoresis to identify biochemical markers to be used in screening large hybrid populations. The systems tested (total proteins and esterases) did not recognize patterns for mode of reproduction, but helped identify the hybrid nature of the progeny, which is sometimes difficult to do when parents are morphologically similar.

A population of first-generation hybrids was produced in Colombia, to verify the validity of the progeny test for determining mode of reproduction of progenitors (Miles and Valle, 1991). Crosses of tetraploid *B. ruziziensis* with tetraploid biotypes of *B. brizantha* and *B. decumbens* resulted in 128 hybrids, which were vegetatively propagated and established as replicated spaced plants in the field. Open-pollinated seed from 107 hybrids was established in a field progeny test, and mode of reproduction was inferred, based on relative uniformity versus heterogeneity of progenies. Parents were also phenotyped by microscopic examination of embryo-sac structures (Table 6).

The two methods agreed closely, except for 10 progenies, in which degree of sexuality (determined by embryo-sac analysis) ranged from 10% to 77%. In these 10, the degree of effective sexuality as detected by the progeny test was not closely associated with the proportion of sexual sacs observed microscopically. It is easy to explain off-types in a facultative apomict with 50% or 70% sexuality, but it is unclear what factors determine that low rates of sexuality, such as 10% or 17%, produce off-types in these progenies. The proportion of sexual to apomictic plants recovered in this test—56:51—does not differ from the 1:1 expected for monogenic control of inheritance of apomixis.

Cross Compatibilities between Species

Three important *Brachiaria* species—*B. decumbens*, *B. brizantha*, and *B. ruziziensis*—seem to belong to the same agamic complex, as hybrids can easily be obtained, once ploidy barriers are overcome (Miles and Valle, Ch. 11, this volume), and these hybrids are completely or largely fertile. The *B. ruziziensis* germplasm screened consists of about 30 accessions, all found to be sexual diploids. Aposporic sacs were never observed, either in the diploids or in the induced tetraploids.

Ndikumana (1985) crossed accessions of these same three species and recovered more hybrids in the ruzi x dec

Table 6. Comparison between progeny test (PT) and embryo-sac analysis (ESA) for determining mode of reproduction for first-generation interspecific *Brachiaria* hybrids.

Identification	Mode of reproduction assessed by		Rate of sexuality by ESA (%)
	PT	ESA	
54 hybrids	Sexual	Sexual	100
37 hybrids	Apomictic	Apomictic	10-73
4 hybrids	Unclassified	Apomictic	7-83
2 hybrids	Unclassified	Sexual	100
Facultative apomicts classified as sexual on PT			
541-03	Sexual	Apomictic	10
544-04	Sexual	Apomictic	50
549-02	Sexual	Apomictic	17
554-02	Sexual	Apomictic	63
554-03	Sexual	Apomictic	77
683-01	Sexual	Apomictic	52
687-01	Sexual	Apomictic	70
693-02	Sexual	Apomictic	47
694-07	Sexual	Apomictic	43
702-06	Sexual	Apomictic	30

SOURCE: Miles and Valle, 1991.

than in the ruzi x bri crosses. Also, after examining chromosome pairing, he concluded that *B. ruziziensis* and *B. decumbens* were closer than *B. ruziziensis* and *B. brizantha*.

Ngendahayo (1988) studied self- and cross-compatibility among these species by examining in vitro pollen tube growth and fertilization. More than 60% of ovaries contained well-developed pollen tubes in ruzi x dec crosses, whereas only 11% showed pollen tube growth in ruzi x bri crosses. Ngendahayo therefore concluded that a compatibility barrier did not exist between *B. ruziziensis* and *B. decumbens*, but was strong in interspecific crosses with *B. brizantha*.

Since then, different accessions of these same three species have been extensively hybridized, both in Brazil (CNPGC/EMBRAPA) and in Colombia (CIAT). Data suggest that compatibility is genotype-dependent, as many more hybrids have been obtained in first-generation crosses of ruzi x bri (cv. Marandu) (227) than of ruzi x dec (cv. Basilisk) (125) in Brazil (Valle and Glienke, 1991).

Recently, other species of *Brachiaria* have been crossed in Brazil (Valle et al., 1994; C. B. do Valle, unpublished data). Crosses at the diploid level between sexual diploids of *B. decumbens* and one accession of *B. brizantha* resulted in three hybrids, all sexual, very vigorous, stoloniferous plants. Other crosses include *B. decumbens* (2x, sexual) pollinated by *B. humidicola* (4x, sexual accession H31); H31 x *B. decumbens* or H31 x *B. brizantha* (4x, apomictic); and H31 x *B. ruziziensis* (4x, sexual). Seeds will be germinated, and the hybrid nature of the progenies, chromosome configuration, and mode of reproduction will then be determined.

Interest in wide hybridization arose because different species of this genus show traits of agronomic importance; for instance, complete antibiosis toward spittlebugs—the most serious pests of *Brachiaria* pastures—has been detected in two accessions of *B. jubata* (Lapointe et al., 1992), and adaptation to waterlogged conditions is present in accessions of *B. humidicola* (apomictic hexaploids).

Conclusions

Team efforts to study recently introduced grasses of the genus *Brachiaria* have already produced significant results:

interspecific hybridization has been accomplished for species of economic importance; inheritance of apomixis has been shown to fit a single-dominant-gene model; new sexual accessions have been discovered; and a large germplasm collection has been assembled, enabling ample selection of agronomically desirable genotypes.

However, several deficiencies in our understanding still constrain efficiency in breeding. These include the regulation of expression of sexuality in apomictic hybrids; the phylogenetic relationships among species; compatibilities between ploidy levels; and the development of inexpensive but efficient screening techniques for mode of reproduction.

The tremendous diversity that has been fixed in apomictic ecotypes is now available for breeding superior varieties with improved forage quality, seed production, resistance to insect pests and diseases, and other traits. Because of simple genetic control, any hybridization between a sexual tetraploid and an apomictic accession releases a wide range of polymorphic hybrids, half of which are fixed indefinitely through apomixis and can therefore be selected, rapidly multiplied, and tested for agronomic performance. With the considerable genetic resources now available, the breeding of *Brachiaria* can be a low-risk and highly profitable enterprise that will have a major impact on animal production in the tropics.

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Chapter 11

Manipulation of Apomixis in *Brachiaria* Breeding

J. W. Miles* and C. B. do Valle**

Abstract

Until 10 years ago, genetic improvement of *Brachiaria* species depended entirely on selection among naturally existing genotypes, genetic recombination being impossible because of prevailing apomictic reproduction. However, recent advances in understanding the genetics and cytogenetics of *Brachiaria*, and the creation of a tetraploid sexual *B. ruziziensis* have opened the way for controlled genetic manipulation. Two relevant gene pools are discussed. Genetic recombination is now possible in the *B. ruziziensis/B. brizantha/ B. decumbens* pool. Breeding in the *B. humidicola/B. dictyoneura/B. jubata* pool awaits the development of a compatible source of sexuality. Present breeding initiatives aim to create apomictic genotypes combining spittlebug resistance and edaphic adaptation with other desirable attributes. Evaluation methods need to be improved. Current breeding schemes for *Brachiaria*, which are described, seek to exploit apomixis. They are empirical, and are based on general principles of quantitative genetics and our current limited knowledge of the inheritance of reproductive mode and other important traits. Clearer definition of relevant breeding objectives and better evaluation methodology will improve the efficiency and effectiveness of *Brachiaria* breeding.

Introduction

About 25 years ago, massive importation of seed of the Australian *Brachiaria decumbens* cv. Basilisk, a selection from a small collection of natural germplasm, greatly enhanced the productivity of pastures on the vast South American savannas, particularly in the Brazilian Cerrados. Although cv. Basilisk is perhaps uniquely adapted and productive on the infertile acid soils typical of the tropical American savannas, its deficiencies soon became apparent. For instance, susceptibility to spittlebug, coupled with failure of sward regeneration because of poor seed viability, eliminated this cultivar from more humid environments. Programs aimed at producing new *Brachiaria* cultivars were initiated, relying initially on collection and introduction of natural germplasm (Grof et al., 1989; Valle et al., 1993a). Five commercial cultivars, all direct selections from natural germplasm collected in Africa, are now available. All have limitations (Lapointe and Miles, 1992; Keller-Grein et al., Ch. 2, this volume), and the identification of attributes needed in new cultivars has been relatively straightforward.

In addition to clearly defined objectives, prerequisites for effective plant breeding are (1) a thorough knowledge of the biology, cytology, and reproductive behavior of the crop; and (2) access to an adequate genetic base. Basic biological knowledge is particularly critical for a "wild" crop such as the *Brachiaria* forage grasses. Valle (1986; 1990) reported results of detailed studies of the cytology and reproductive behavior in several *Brachiaria* species, providing a solid basis for breeding work when a large new germplasm collection became available in the late 1980s (Keller-Grein et al., Ch. 2, this volume).

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Because the commercial species were predominantly apomictic (Schank and Sotomayor-Rios, 1968; Sotomayor-Rios et al., 1960; Valle, 1986), genetic improvement based on the combination of attributes from two or more parental genotypes by conventional hybridization was not directly possible. However, despite the obstacle it offers to genetic recombination, apomixis has significant potential as a tool in plant breeding, in that even highly heterozygous genotypes breed true through seed (Bashaw, 1980a; Bashaw and Funk, 1987; Hanna and Bashaw, 1987).

Implications of Apomictic Reproduction

Apomixis is generally understood as asexual reproduction in plants through seed. Early studies of reproductive mode in *Brachiaria* (Bogdan, 1959; Brown and Emery, 1958; Pritchard, 1967) identified apomixis in several species. If obligate, apomixis poses a formidable obstacle to conventional genetic recombination. However, apomixis is seldom, if ever, completely obligate, either at the level of the individual or of the species (Nijs and Dijk, 1993). Expression of apomixis is often incomplete, and some seeds contain embryos that have arisen from meiosis and fertilization. In most apomictic species, fully sexual genotypes have been found in the same or a closely related species. A frequent pattern is that diploids are obligately sexual, different degrees of apomixis being found among related polyploids (Asker and Jerling, 1992; deWet and Harlan, 1970; Quarin and Norrmann, 1987; Valle, 1990; Valle et al., 1989). Schank and Sotomayor-Rios (1968) and Sotomayor-Rios et al. (1970) reported sexual reproduction in *B. ruziziensis*, and Ferguson and Crowder (1974) confirmed that this species is naturally diploid and obligately sexual.

Where a mechanism for genetic recombination is available through residual sexuality in facultative apomicts or in cross-compatible, fully sexual genotypes, powerful breeding schemes are potentially available. These would produce novel genetic combinations by conventional hybridization and, furthermore, would also fix these hybrid genotypes and propagate them indefinitely through seed.

To date, only modest plant breeding efforts have been conducted in apomictic species, primarily in several genera of tropical forage grasses in which apomixis occurs naturally. However, the potential of apomictic reproduction is becoming better appreciated, and cross-compatible sexual genotypes are being identified or produced. These developments, along with better tools to assess reproductive mode, have stimulated plant breeding efforts in apomictic species (Nijs and Dijk, 1993). Numerous efforts have been made to introduce apomixis from wild relatives into sexually reproducing crop species, for example, pearl millet (*Pennisetum glaucum* L.), maize (*Zea mays* L.), and wheat (*Triticum* spp. L.) (Carman, 1992).

Achieving Genetic Recombination in *Brachiaria*

Artificial hybridization in *Brachiaria* has been sought at least since the early 1970s, when Ferguson and Crowder (1974) attempted to produce hybrids by pollinating diploid, sexual *B. ruziziensis* with pollen from a tetraploid, apomictic *B. decumbens*. This early attempt was unsuccessful, owing, apparently, to the difficulty of crossing the ploidy barrier. Ferguson and Crowder (1974) suggested developing a sexual plant compatible with the tetraploid apomicts by artificially doubling the chromosome number of the naturally diploid sexual *B. ruziziensis*.

Hacker (1988) successfully crossed a diploid, sexual *B. decumbens* with a tetraploid, apomictic one. The resulting hybrid was triploid and completely sterile, and hence represented a genetic dead end. Hacker suggested two alternative approaches to overcoming the ploidy

barrier between sexual diploids and apomictic tetraploids in *Brachiaria*: (1) colchicine treatment of the sterile triploid hybrid to produce a fertile allohexaploid; (2) colchicine treatment of the sexual diploid to produce a sexual tetraploid cross-compatible with tetraploid apomicts.

Exploiting apomixis in *Brachiaria* breeding became possible through the work done at the Catholic University of Louvain in Belgium in the early 1980s. An obligately sexual tetraploid was successfully developed by colchicine treatment of sexual diploid *B. ruziziensis* (Gobbe et al., 1981; Swenne et al., 1981). The Belgian material is still the basis of all ongoing breeding work in *Brachiaria*, although efforts to produce additional fully sexual tetraploids by conventional colchicine treatment or by tissue culture of sexual diploids have continued (C. B. do Valle, 1994, unpublished data).

Hybridization with the newly available sexual tetraploid was quickly begun. Ndikumana (1985) reported successful interspecific hybridization in crosses using the tetraploid sexual *B. ruziziensis* and two tetraploid apomictic accessions each of *B. decumbens* or *B. brizantha* as pollinators. Hybrids were confirmed by the presence of paternal morphological traits. In producing hybrid plants from pollinations of the sexual tetraploid *B. ruziziensis* by tetraploid apomictic *B. decumbens* or *B. brizantha*, Ndikumana demonstrated empirically the relatively close phylogenetic relationships among these three species.

Although the resulting population of hybrids was small (a total of 35 individuals), analysis of their reproductive mode by embryo-sac analysis suggested simple genetic control of apomixis (Ndikumana, 1985).

Although this pioneering Belgian work opened up the possibility of genetic improvement of *Brachiaria* (Gobbe et al., 1983), it was only after the tetraploid, sexual *B. ruziziensis* reached Brazil in 1988 that this potential began to be realized in applied breeding programs.

The first major *Brachiaria* hybridization programs developed in Brazil (CNPGC/EMBRAPA) and in Colombia (CIAT). The feasibility of large-scale hybridization in the field was demonstrated by Calderón and Agudelo Cortés (1990), who obtained more than 90% hybrid offspring from potted tetraploid sexual plants allowed to open-pollinate in a field of flowering *B. decumbens* or *B. brizantha*. These authors present convincing isozyme evidence for the hybrid nature of progenies resulting from interspecific pollination (Figure 1).

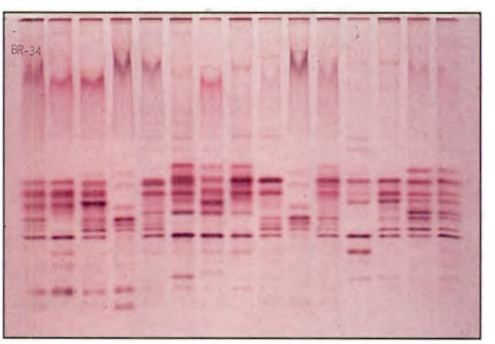

Figure 1. Electrophoretic alpha-, beta-esterase banding patterns, confirming hybridity. Column 2 = sexual, female parent: tetraploidized *B. ruziziensis*. Column 4 = apomictic, pollen parent: *B. brizantha* CIAT 6387. Column 3 = hybrid, showing paternal bands, which are absent in sexual maternal. Column 5 = a different hybrid between tetraploidized, sexual *B. ruziziensis* and *B. brizantha* CIAT 6387. Column 13 = hybrid between tetraploidized, sexual *B. ruziziensis* (column 12) and *B. decumbens* CIAT 606 (column 14). Note presence of paternal bands in hybrid, which are absent from the sexual maternal.

Inheritance of Apomixis

While simple genetic models for the inheritance of apomixis have been proposed for several natural apomictic species, such as *Panicum maximum* (Savidan, 1983) and *Cenchrus ciliaris*

(Sherwood et al., 1994), the evidence supporting monogenic determination of apomixis in *Brachiaria* was, until recently, limited to the analysis of Ndikumana's small hybrid population. Breeding work, therefore, commenced on an empirical basis as additional data accumulated. Even in species where the mechanism of inheritance of reproductive mode was unknown at the time, hybridization followed by selection of apomictic clones from resulting progenies led to the development of new cultivars, for example, in *C. ciliaris* (Bashaw, 1968; 1980b; Taliaferro and Bashaw, 1966) and *Poa pratensis* (Bashaw and Funk, 1987; Nijs and Dijk, 1993; Pepin and Funk, 1971). However, the development of efficient, long-term breeding schemes would be greatly facilitated by a rigorous, detailed understanding of the genetics of apomixis.

Our current understanding of genetic control of apomixis in the *B. ruziziensis/B. decumbens/B. brizantha* complex has been expanded greatly by the work of Valle and collaborators. Their detailed crossing program and analysis of reproductive mode of first- and second-generation hybrids, backcrosses, and selfed progenies are reported by Valle and Savidan in Ch. 10 of this volume. Recent results demonstrating cosegregation of random amplified polymorphic DNA (RAPD) markers with reproductive mode phenotype (Tohme et al., Ch. 13, this volume) render even more convincing a monogenic model of inheritance.

However, any complete model of inheritance of reproductive mode in *Brachiaria* must account for the essentially continuous range in expression of apomixis in sexual x apomictic hybrid progenies, where individuals in that 50% of the population expressing any degree of apomictic reproduction range from highly sexual facultative apomicts to essentially obligate apomicts. We hypothesize some unknown (but perhaps large) number of segregating genes, which, to some degree or other, modify the expression of a single gene conferring the potential for apomictic reproduction. This model remains to be tested by examining the parent-progeny correlation for degree of expression of apomixis in a series of hybrid progenies, produced by crossing a single, fully sexual clone with paternal genotypes differing in degree of apomictic expression.

Brachiaria Gene Pools

At least two gene pools of actual or potential relevance to plant breeding are recognized in *Brachiaria*. Analysis of genetic relationships in the genus, based on morphological characters (Valle et al., 1993b; Renvoize et al., Ch. 1, this volume) or molecular markers (Tohme et al., Ch. 13, this volume), confirms the phylogenetic proximity of *B. ruziziensis*, *B. decumbens*, and *B. brizantha*. Based on hybrid seed set and viability of hybrid seedlings and chromosome pairing in hybrids, Lutts et al. (1991) found that *B. ruziziensis* is more closely related to *B. decumbens* than to *B. brizantha*. While significant levels of sterility are observed in some interspecific hybrid combinations, indicating species incompatibilities (Lutts et al., 1991; Valle et al., 1994), many interspecific crosses within this species complex have been successful (J. W. Miles and C. B. do Valle, unpublished data). Meiotic chromosome behavior of hybrids and the relative ease with which interspecific hybrids are made (Lutts et al., 1991) suggest that germplasm assigned to these three species forms a more or less coherent gene pool, once ploidy barriers are overcome.

Brachiaria humidicola is a commercially important species that falls into a distinct taxonomic group (Renvoize et al., Ch. 1, this volume). Furthermore, the commercial cultivars Llanero and Tully are apomictic hexaploids (Valle, 1986); hybridization of these two lines with existing sexual tetraploids in the *B. ruziziensis* complex has not even been attempted. True *B. dictyoneura* is moderately close to *B. humidicola*, and hybridization between them may

eventually be possible, if a closely related sexual hexaploid can be found or developed. A natural sexual tetraploid has been identified in *B. humidicola* (Valle and Glienke, 1991), and several approaches are being attempted to introduce sexuality into the hexaploid *B. humidicola* complex.

Another *Brachiaria* species, *B. jubata*, has potentially useful insect resistance, although it is not currently used commercially (Lapointe et al., 1992). Both diploid and tetraploid (sexual and apomictic) genotypes have been identified within the species (Valle, 1990). Attempts to hybridize *B. jubata* with sexual material of the *B. ruziziensis* complex have yielded very few putative hybrid plants. The fertility and reproductive behavior of these have not been determined, nor has the potential for gene exchange between *B. jubata* and existing populations in the *B. ruziziensis* complex. *Brachiaria jubata* may hybridize more successfully with *B. humidicola* or *B. dictyoneura* than with the *B. brizantha* complex (Renvoize et al., Ch. 1, this volume).

Limitations of Existing Genotypes of Brachiaria

Given that genetic recombination is now feasible, are *Brachiaria* breeding programs really necessary? All existing commercial cultivars have recognized defects (Keller-Grein et al., Ch. 2, this volume), mainly susceptibility to biotic stresses or poor edaphic adaptation (Lapointe and Miles, 1992). The initial evaluation of the new influx of natural *Brachiaria* germplasm has uncovered interesting new variation; however, it now appears unlikely that the ideal, universal *Brachiaria* cultivar will be found for every environment and production system. Although a desired combination of resistance to biotic and edaphic stresses may possibly arise from natural selection, natural selection is unlikely ever to favor genotypes with high forage quality—an attribute of considerable value in agriculture but one that does not necessarily improve fitness in nature. Given the absence of other forage grasses with comparable potential on vast areas of acid soils, we judge breeding work to be fully justified. New cultivars are needed to complement or replace existing ones derived directly from wild germplasm collected from nature. As ruminant production systems become more intensive, greater and more diverse demands will be placed on *Brachiaria* cultivars, which only directed plant breeding can meet.

Breeding Objectives

Objectives of existing *Brachiaria* breeding programs follow from recognized deficiencies in existing commercial cultivars and germplasm accessions. Put simply, the initial objective is to develop an apomictic cultivar combining the persistence, productivity, and adaptation to infertile acid soils of common *B. decumbens* cv. Basilisk with durable antibiotic resistance to spittlebugs (Homoptera:Cercopidae), which are its principal biotic constraint (Valério et al., Ch. 6, this volume).

Additional attributes would be desirable in any bred *Brachiaria* cultivar. Resistance to rhizoctonia foliar blight (caused by *Rhizoctonia solani*) and rust (caused by *Uromyces setariae-italicae* and/or *Puccinia levis* var. *panici-sanguinalis*) should be at least as good as that of cv. Basilisk. Marked differences in resistance to leafcutting attine ants (Hymenoptera:Formicidae) have been demonstrated among currently available *Brachiaria* cultivars (Corrales, 1993; Valério et al., Ch. 6, this volume); this resistance has been shown to be associated with an inhibitory effect of leaf extract on the fungus "cultivated" by these ants. A simple screening technique based on in vitro fungal growth rate on aqueous extract of leaves correlates with effects of different forage grass genotypes on ant colony number and size in the field (Corrales, 1993; Valério et al., Ch. 6, this volume).

Forage yield and forage quality will influence productivity per hectare or per head, respectively on improved *Brachiaria* pastures. Antiquality attributes have been associated with existing *Brachiaria* cultivars. Photosensitization, the cause of which is not fully understood, is common in animals, particularly the young, grazing pastures of cv. Basilisk. High oxalate content in *B. humidicola* can cause a "swollen face" syndrome in horses (Lascano and Euclides, Ch. 7, this volume).

A wide range in flowering response has been recorded in *Brachiaria,* and it should be possible to identify recombinants with any desired photoperiodic response and flowering time in a particular environment. Seed yield and quality (dormancy) and seedling vigor are important for propagation. However, seed yield of existing cultivars may be adequate for the current economic environment and seed production systems (Hopkinson et al., Ch. 8, this volume). Whether an effort to reduce seed dormancy genetically is warranted or even desirable is not entirely clear. Seed dormancy in existing cultivars, except perhaps in cv. Llanero, is not seen as a major deficiency (Hopkinson et al., Ch. 8, this volume), and genetic elimination of dormancy may have detrimental effects on pasture establishment and persistence. Uneven seed maturity and shattering are often seen as a limitation to high seed yield. However, current methods of recovery of fallen seed from the soil surface may be adequate, and may even give a product superior to combine-harvested seed (Hopkinson et al., Ch. 8, this volume).

Nitrogen fixation is generally considered an attribute important only in legumes. However, recent work in Brazil has demonstrated a significant level of N_2-fixation by bacteria associated with grasses, including several *Brachiaria* species (Boddey and Victoria, 1986; Boddey et al., Ch. 5, this volume). Furthermore, intraspecific genetic differences have been shown in the grass host (*P. maximum*) in the ability to support and benefit from fixed N (Miranda and Boddey, 1987; Miranda et al., 1990). If efficient methods can be developed to measure these differences on large segregating populations, then this potential source of biologically derived N may be more fully exploited in new *Brachiaria* cultivars.

Sources of desired attributes

The *B. ruziziensis*/*B. decumbens*/*B. brizantha* complex. A wealth of genetic variation exists within this complex. Spittlebug resistance has been identified in several germplasm accessions, as well as in the commercial *B. brizantha* cv. Marandu (Lapointe et al., 1992). Preliminary evidence suggests that resistance is highly heritable. Miles et al. (1995) found significant variation among half-sib families for adult damage scores under natural field infestation ($h^2 = 0.44 \pm 0.098$) and high correlation of nymphal survival between pollen parent and topcross progeny ($r^2 = 0.897$; $n = 11$). Reasonably efficient screening methods for nymphal survival (a measure of antibiosis) have been developed (Ferrufino and Lapointe, 1989; Lapointe et al., 1992; Valério et al., Ch. 6, this volume), and spittlebug resistance should be easily manipulated in the breeding program, unless resistance is found to be negatively correlated with other desirable traits.

Common *B. decumbens* is widely recognized as having broad adaptation to infertile acid soils. The mechanisms of genetic control of edaphic adaptation are unknown, but are probably complex. The soil factors for which tolerance is required are also being investigated (Rao et al., 1993; Rao et al., Ch. 4, this volume), and efficient screening methods will probably have to await the results of this research.

A wide range of in vitro dry matter digestibility (IVDMD) has been shown among accessions of natural *Brachiaria* germplasm (Nicodemo et al., 1991;

Lascano and Euclides, Ch. 7, this volume). Concern has been expressed about possible negative association between nutritional quality and spittlebug resistance. However, the feed quality of the highly resistant cv. Marandu is nearly as good as that of the susceptible common *B. decumbens* (Lascano and Euclides, Ch. 7, this volume). Greater attention will have to be paid to quality attributes as populations with the required combination of edaphic adaptation and spittlebug resistance are developed.

Brachiaria brizantha is a highly diverse species (S. A. Renvoize, 1993, unpublished report) and a reasonable germplasm collection now exists (Lapointe and Miles, 1992; Keller-Grein et al., Ch. 2, this volume). It seems unlikely that useful genetic variation will be exhausted shortly.

The *B. humidicola/B. dictyoneura* complex. Commercial cultivars in the *B. humidicola/ B. dictyoneura* group are very vigorous, strongly stoloniferous, and competitive. However, nutritional quality, particularly N content, is low (Lascano and Euclides, Ch. 7, this volume). *Brachiaria humidicola* shows poor flowering and seed production at low latitudes (Hopkinson et al., Ch. 8, this volume). Cultivars Tully and Llanero are tolerant of spittlebug attack, but both are good hosts (Lapointe et al., 1992). A reasonable collection of germplasm accessions of *B. humidicola* and *B. dictyoneura* now exists (Keller-Grein et al., Ch. 2, this volume), and interesting new variation is being documented, particularly in terms of forage quality (IVDMD and crude protein content) (CIAT, 1993; Lascano and Euclides, Ch. 7, this volume). However, until a compatible source of sexuality is found for this complex, breeding activities will be frustrated.

Breeding schemes exploiting apomixis

The methods currently employed in *Brachiaria* breeding programs are based on general principles of quantitative genetics and on the limited information available on genetic control of reproductive mode and other desirable traits. They aim to produce and identify apomictic plants with desirable combinations of attributes not found in accessions of natural *Brachiaria* germplasm.

We assume that apomictic accessions are highly heterozygous—an assumption supported by the wide variation among F_1 progenies resulting from biparental crosses—and that most (if not all) attributes of interest are quantitatively inherited.

Information available to date on genetic control of reproductive mode (Valle and Savidan, Ch. 10, this volume) suggests that the potential for apomictic reproduction is conditioned by a single dominant gene whose expression is determined by other, perhaps many other, modifying genes.

Ngendahayo et al. (1988) found a relationship between reproductive mode and degree of self-compatibility, based on pollen-tube growth in *Brachiaria* accessions and hybrids. Apomictic genotypes, whether parental or hybrid, were more self-compatible than sexual genotypes. Because apomictic species of *Brachiaria* are pseudogamous (i.e., require pollination for endosperm formation), self-incompatibility would have a distinct disadvantage in nature, where a single successful apomictic clone might cover a large area. Predominant outcrossing was found for sexual tetraploid *B. ruziziensis*. More than 90% of the open-pollinated seed harvested from pot-grown plants of tetraploid sexual *B. ruziziensis* set into a field of 4x *B. decumbens* at flowering were hybrid (Calderón and Agudelo Cortés, 1990).

Because of the narrow base of tetraploid sexual germplasm, it was reasonable to expect that more than one cycle of hybridization would be needed to achieve the desired combination of characters. The Belgian tetraploid sexual

is not only extremely susceptible to spittlebug, but also has poor edaphic adaptation. Hence, we envision accumulating favorable alleles over several cycles of recurrent selection and recombination.

Two types of breeding populations are being formed. The simplest form of population improvement would be in heterogeneous populations homozygous for sexuality, where simple mass selection or half-sib family selection could be practiced as in any allogamous crop species (Figure 2). Such populations have been formed in Brazil and Colombia by intercrossing selected, fully sexual, hybrid clones (CIAT, 1993), and are being subjected to recurrent selection. The improved populations will have to be crossed subsequently with appropriate apomicts to recover apomictic segregants for development to cultivar status.

A second approach has been to improve both apomicts and sexuals simultaneously in a single population that segregates for reproductive mode (Figure 3). Simple, monogenic control of apomixis makes this scheme feasible. The

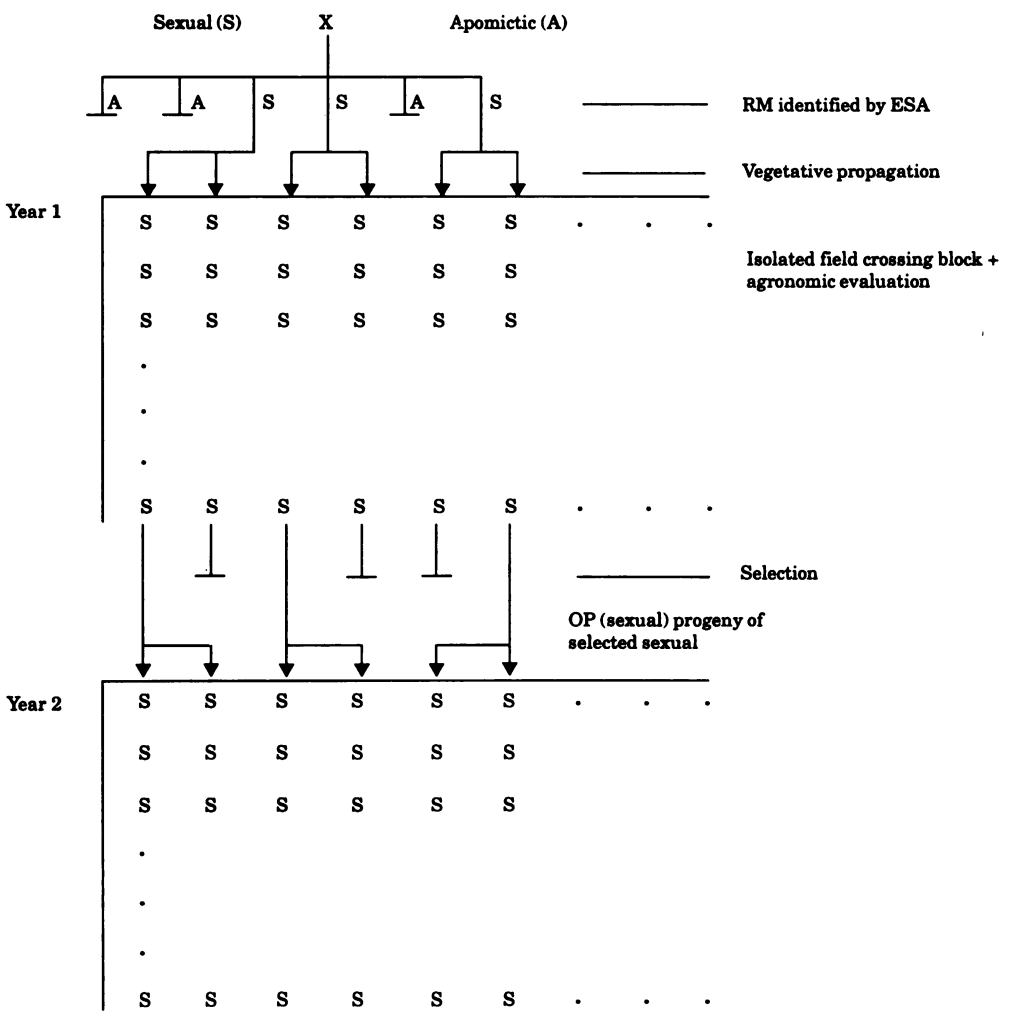

Figure 2. Simplified diagram of recurrent mass selection employed for a sexual *Brachiaria* population at CIAT. (ESA = embryo sac analysis; RM = reproductive mode; OP = open-pollinated.)

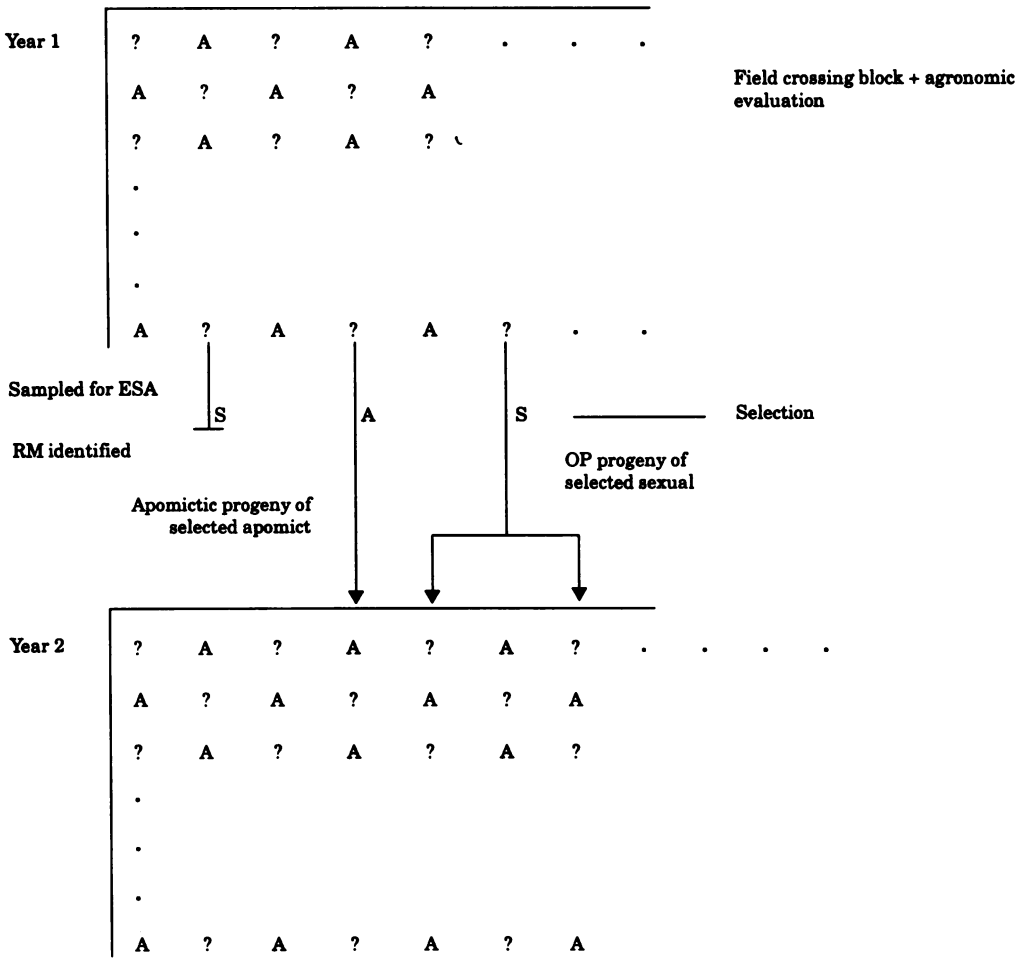

Figure 3. Simplified diagram of recurrent selection scheme employed in an apomictic/sexual *Brachiaria* population at CIAT. (A = known apomict; ? = hybrid progeny with unknown RM; S = sexual; ESA = embryo sac analysis; RM = reproductive mode; OP = open-pollinated.)

crossing block consists of known apomicts, randomly assigned to alternate positions of a square grid to serve as pollinators. The remaining positions are planted to the open-pollinated progeny of sexual plants from the previous cycle's crossing block. These progenies will contain both sexual and apomictic individuals. However, reproductive mode cannot be distinguished at the moment of planting. At flowering, the individuals in open-pollinated progenies are sampled for embryo-sac analysis, and seed is harvested from individual plants. To complete the cycle, the open-pollinated progeny of selected sexuals and the progenies of selected apomictic segregants are established in the subsequent crossing block.

In early cycles of selection, all degrees of expression of apomixis have been observed. Assuming that our model of a single "apomixis gene" and modifiers is correct, it ought to be possible to select for enhanced expression of this gene, as for any other quantitatively inherited trait, by choosing as apomictic pollinators

only "good" apomicts and culling all highly sexual facultative apomicts.

Because our ultimate objective is to exploit heterosis through apomixis in superior hybrid genetic combinations, selection on specific combining ability or some form of reciprocal recurrent selection may be more appropriate than the intrapopulation selection schemes now being used. For an interpopulation selection scheme, one of the populations would probably contain both reproductive modes, while the other could be homozygous sexual. Selection in a sexual population on combining ability with one (or more) elite apomictic clones would be reasonably straightforward.

Details of efficient evaluation, selection, and hybridization schedules have yet to be worked out. We need to know much more about the genetics of important traits, including a complete genetic model for control of reproductive mode, before optimal schemes can be designed.

Screening methods

The special problems of breeding forage plants (e.g., the complex criteria of merit, the high cost of realistic evaluation of animal performance) have been dealt with in various reviews (Bray, 1975; Bray and Hutton, 1976; Cameron, 1983; Clements, 1989) and will not be treated in detail here. Developing more efficient methods to assess edaphic adaptation and pasture persistence is of particular concern in *Brachiaria* breeding work. This is not likely until we have a much better understanding of the factors conferring adaptation to infertile acid soils (Rao et al., 1993).

Artificial infestation of greenhouse-grown plants has enabled much more precise assessment of spittlebug resistance than that achieved by natural infestation in the field, which is notoriously variable (Ferrufino and Lapointe, 1989; Lapointe et al., 1989; 1992; Valério et al., Ch. 6, this volume). However, our present capacity to handle the large volume of segregants generated in the breeding programs is only marginally adequate (Miles et al., 1995) and improved methods, perhaps based on understanding of the biochemical basis of resistance, would be desirable.

Assessment of reproductive mode

The efficiency of any breeding program seeking apomicts will be improved by quicker, cheaper, and more reliable methods to assess reproductive mode in segregating populations. Progeny testing is inadequate for reliable identification of facultative apomicts (Miles and Valle, 1991). Ovary clearing techniques (Young et al., 1979) are a marked improvement over former methods of fixing and thin-sectioning; however, they still entail considerable time and labor, and have a major disadvantage in that reproductive mode cannot be determined until flowering.

A reliable molecular marker tightly linked to the gene conferring apomixis potential would be useful (Tohme et al., Ch. 13, this volume). Our present understanding of the genetics of apomixis suggests that it should be possible to find such a marker to identify obligate sexuals (by the absence of the marker) in segregating populations. Such a marker would permit a 50% reduction in the volume of embryo-sac analyses needed to support the breeding program.

A hypothetical development that would be extremely useful in breeding any apomictic plant, including *Brachiaria,* would be a simple mechanism to turn the apomixis gene on or off at will. In theory, this should be possible, but it is unlikely to be available in the short term.

Future Developments

We need improved evaluation and selection methodologies for nearly all traits of agronomic importance,

particularly spittlebug resistance and edaphic adaptation. At present, the design of genetically and economically efficient breeding schemes for apomictic species is at a frankly empirical stage. This topic has not received attention from applied quantitative geneticists, but will become increasingly relevant to plant breeding as apomixis is transferred into other crop species.

The *B. humidicola/B. dictyoneura* complex is commercially valuable but inaccessible to plant breeding because of the lack of compatible sexual hexaploid biotypes. Several approaches are being considered to break the apomixis barrier so that important breeding objectives can be pursued within this complex.

The development of simple mechanisms to control expression of apomixis would be a tremendous advance for breeding *Brachiaria*, as well as other apomictic species.

Applied breeding of *Brachiaria* is now an established activity, with major programs in both Brazil and Colombia (Valle and Miles, 1992; 1994). These are still in a formative stage, and neither has yet resulted in the release of a commercial cultivar. However, they are steadily generating the information and experience on which future routine breeding of apomicts will be based. The programs have access to a broad range of genetic diversity in three species. We are optimistic that the serious deficiencies of existing cultivars will be rectified as the desired character combinations are identified in apomictic recombinants, and these are developed to cultivar status.

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To save space, the following acronyms are used in place of publishers' names:

ASA = American Society of Agronomy

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

INRA = Institut national de la recherche agronomique

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Agricultural Science

NZSAP = New Zealand Society of Animal Production

TGSA = Tropical Grasslands Society of Australia

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Chapter 12

Theoretical Potential of Biotechniques in Crop Improvement

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Abstract

For the past decade, biotechnology has been promising to deliver new methods and new types of variation to the plant breeder, but only in the last 2 or 3 years has this become a reality. A wide array of new molecular biology and genetic manipulation techniques is now available, which should enable plant breeders to produce improved plants more easily and to develop varieties and cultivars with higher and more sustainable yields, improved quality and composition, greater resistance to pests and diseases, and improved tolerance of climatic and edaphic stresses. Opinions on the use of genetic manipulation differ widely, but in our view, any technology that helps extend the range of variation and manipulate the genetic material of the plant has a role to play in developing new and improved crops. Obstacles that still exist in the application of biotechnology, particularly to important cereals and grasses, are likely to be overcome soon. Improvements will result from the application of a range of technologies, from those giving rise to single base changes to those that modify whole genomes. To effect these changes, plant breeders need to understand the potential of biotechnology, and biotechnologists, of the needs of breeders.

Introduction

Plant breeding began when man first consciously selected and saved seed for growing the following season. Since those early times, breeding progressed relatively slowly and, in most instances, was applied only to the major grain and horticultural crops. Forages were neglected until the end of the eighteenth century, when the value of certain well-adapted local ecotypes, such as Devon Eaver ryegrass and Flamande lucerne, was recognized. Early this century, forage breeding followed the traditional approach of ecotype selection. Rapid progress began with the pioneering work at the Welsh Plant Breeding Station in the UK, by Sir George Stapledon and his colleagues (Tyler et al., 1992). The principles that they established for forage improvement were based primarily on the recognition of three factors: first, the importance of genetic variation; second, the reproductive system of the species concerned; and, third, the nutritional requirements of livestock.

The subsequent progress in forage breeding was also stimulated by the application of novel technologies: developments in the design and analysis of field experiments; improved procedures for collection, conservation, and characterization of forage germplasm; cytological analysis and restoration of fertility in hybrids; and the use of biometrical genetic procedures to aid selection of superior genotypes. Against this background we consider the objectives of a breeding program, whether they may be achieved by using traditional breeding methods, and, if not, how biotechnology may assist the breeder. We then discuss the potential role of biotechnology in forage grass improvement.

The primary requirements of any breeding program are twofold: a source of variation and the means to manipulate that variation. The first requirement has

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traditionally been met by the use of naturally occurring adaptations. Considerable variation is still available that can be exploited, particularly when germplasm is manipulated through the classical procedures of hybridization, polyploidy, and recombination through normal sexual processes. The selection of superior genotypes is based on their identification by phenotypic methods, which may then be followed by progeny testing. Superior lines are identified for an inbreeding species, individuals for an apomictic one, and mother plants of a synthetic for an outbreeder. The demands of current plant breeding, however, often require the incorporation of characteristics that cannot be met by these classical means. Breeders must then see what new technologies can offer in terms of variation and its effective manipulation.

The application of biotechnology to forage grasses potentially involves a wide range of procedures, such as genome analysis and the construction of genetic maps, somaclonal variation, androgenesis, and transformation. These are all underpinned by the basic science of molecular biology, which aims at understanding the organization of the genome and identifying genes controlling the physiological and biochemical processes underlying traits of agronomic importance. This knowledge of the basic biology of forage grasses will enhance our ability to relate phenotype to genotype and thus to employ biotechnology more effectively to extend and manipulate variation.

Biotechnology can therefore contribute to plant breeding in three direct ways: first, by providing new techniques that aid conventional breeding; second, by creating new sources of variation; and, third, by increasing our basic understanding of the function and regulation of plant genes.

Figure 1 outlines some of the basic questions that every breeding program

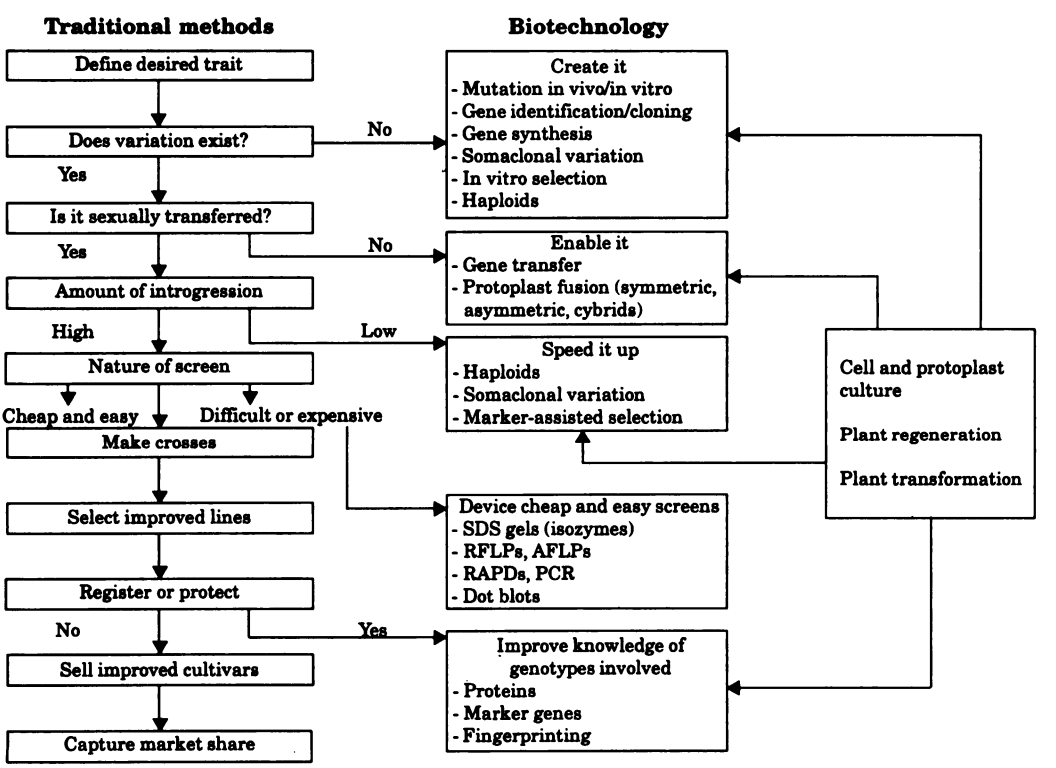

Figure 1. Decision tree for plant breeders and biotechnologists (modified from Miflin, 1988).

must address, together with some of the possible biotechnological solutions. However, before these procedures can be applied, the crop must meet three requirements: first, there must be an adequate system for tissue culture and regeneration; second, transformation systems should be available for the species concerned; and, third, the desired genes should be readily available.

Creation of New Variation for the Desired Trait

Many of the methods developed to create new variation rely heavily on a combination of molecular biology techniques to identify and clone new genes and on effective tissue culture techniques. A wide range of techniques has been developed to allow plant regeneration from diverse tissues, such as embryos, microspores, calli, cell suspensions, and protoplasts (Figure 2). Most of these have been applied to economically important temperate grasses, with varying degrees of success. Regeneration protocols have been worked out for five *Brachiaria* species (Tohme et al., Ch. 13, this volume). Some of these techniques aim to create or release variation from within the existing genome, such as anther and microspore culture or somaclonal variation linked with in vitro selection. Other techniques have been developed to transfer alien genes by other than sexual means, such as via genetic transformation or protoplast fusion.

Gene identification and cloning

Traditionally, gene isolation is based on identifying a gene function and then isolating the protein products. This approach, however, is limited by the fact that many gene products are unknown, present in low concentrations, or difficult to isolate and purify. Molecular approaches based on construction and screening of genomic or cDNA libraries can also be used to clone specific genes, particularly if such genes have been

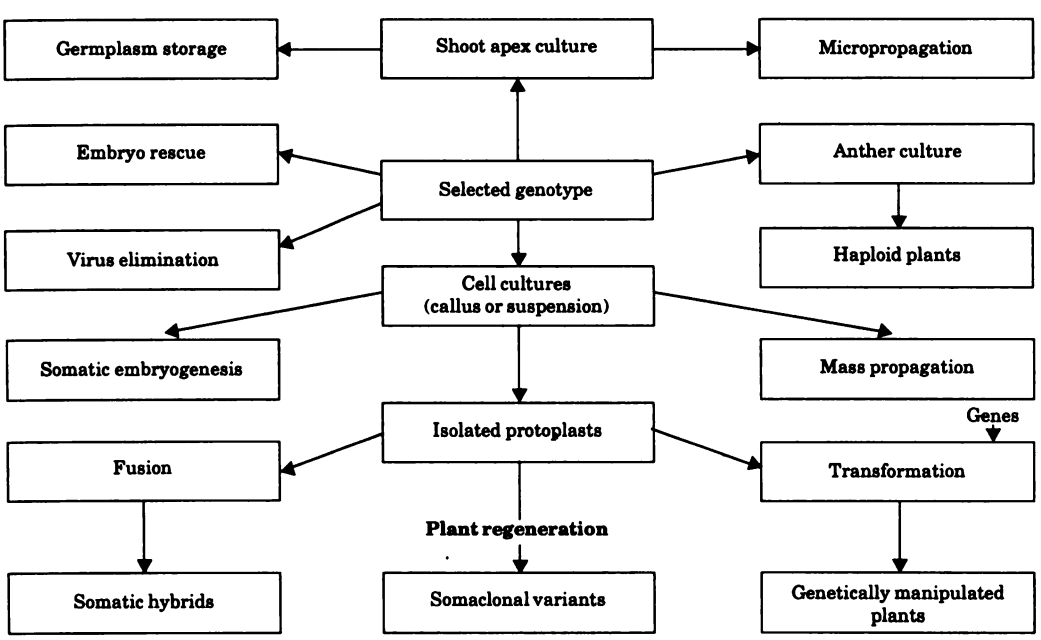

Figure 2. Applications of plant tissue and cell culture to plant breeding and biotechnology.

cloned previously from other species. However, this application is now being superseded by various modified polymerase chain reaction (PCR) protocols that use degenerate primers for conserved gene sequences to clone homologous genes. Two other strategies with great potential for identifying and cloning agronomically important genes are insertional mutagenesis and map-based cloning.

Insertional mutagenesis. Insertion of a foreign gene into the genome of a plant is usually random; hence, such insertions can be at the site of functional genes and can cause disruption. The most widely recognized phenomena of this type are brought about by the germinal or somatic excision of transposons and their reintegration into the genome, often into other genes. When this results in a scorable mutant phenotype, it is often possible to identify the respective gene, using the transposon as a DNA probe. This method of transposon mutagenesis is currently receiving particular attention because it allows mutant genes to be cloned.

A similar system of gene-tagging mutants has also been developed by using insertional mutagenesis where plasmid or T-DNA is inserted into the genome by transformation, and regenerated plants screened for mutants. This is less effective, but probably easier to achieve, than transposon mutagenesis, because the inserted plasmid or T-DNA, unlike transposons, cannot be induced to germinally excise and reintegrate. Thus, each transformation event is unique, and a highly efficient system is required to generate the large number of plants needed for identifying mutants. This technique is also best applied to species that have a small diploid genome, such as *Arabidopsis thaliana* or *Lotus japonicus*. For both these reasons, these techniques are not likely to have immediate applicability to *Brachiaria*. However, once isolated from the "model" species, new molecular biology techniques, such as the PCR, can be used to clone homologous genes from the species of interest.

Map-based cloning. The development of a densely saturated genetic map with markers tightly linked to the gene of interest opens up the possibility of map-based gene cloning (Tanksley et al., 1989). The procedure consists of developing a suite of DNA clones from between the flanking markers, which should contain the gene of interest. This is generally carried out in yeast by creating artificial chromosomes (YACs). The clone containing the gene of interest can be identified by the phenotype of plants transformed by it. This strategy is now being adopted in some crop species, such as rice, where a YAC library of about 12,000 inserts has been produced, covering, it is hoped, the bulk of the genome (Umehara et al., 1993). The recent findings of synteny between rice and wheat (Kurata et al., 1994) and between these species and other members of the Gramineae, such as *Lolium* and *Festuca* (J. W. Forster and M. D. Hayward, unpublished data), opens up the opportunity for isolating genes from apparently unrelated species for use in transformation.

Somaclonal variation

Theoretically, all plants regenerated from cells and tissues should be identical to the parental plant. But the very process of plant regeneration can disrupt the genetic stability of the cells, creating new genetic variation. Such changes are referred to as somaclonal variation (Scowcroft and Larkin, 1982). This variation can exist as gross cytological changes (such as translocations, deletions, or inversions) or more subtle changes (such as point mutations and rearrangements); it may be useful in creating novel variants (Evans, 1989; Lal and Lal, 1990).

Various factors influence somaclonal variation. Choice of tissue for culture, constituents of the medium, and duration of culture all affect genetic stability of regenerants. Less variation exists in plants that have regenerated from preexisting meristems, such as shoot or root meristems, than in those produced

from less organized suspension cultures or from isolated protoplasts (Figure 3). More variation can be tolerated by polyploid than by diploid species. Therefore, regenerants must be closely monitored to establish the expected frequency and types of somaclonal variants created by a given regeneration system. However, for this variation to be used, it must first be identified and then shown to be stably heritable. Many of the biochemical and molecular biology techniques discussed later, such as molecular fingerprinting and the techniques used in marker-assisted selection, can be used to achieve this.

A particular form of somaclonal variation that may be highly practical is the increased degree of interchange between genomes arising from the high incidence of chromosome breakage and reunion which may occur in culture. For example, plants regenerated from cell suspension cultures of *Lolium*

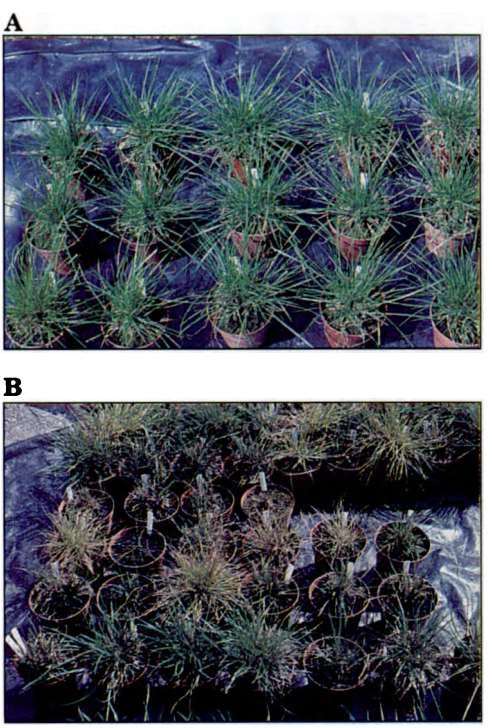

Figure 3. Plants regenerated from (A) cell suspension cultures and (B) isolated protoplasts of *Lolium perenne*.

multiflorum x *Festuca arundinacea* hybrids showed an increased number of culture-induced intergeneric translocations and levels of nonhomologous chromosome association (Humphreys and Dalton, 1992).

The potential for generating and recovering useful somaclonal variation in *Brachiaria* is unknown. No obvious variation was detected in the small populations of plants regenerated in early studies. Furthermore, the successful exploitation of what is essentially random variation will require extremely efficient screening procedures.

In vitro selection

Somaclonal variation can be exploited to select, in vitro, mutant cells with increased tolerance of a wide variety of chemical and environmental stresses (Dix, 1990). Many early studies reported successful in vitro selection from callus and cell suspension cultures exposed to fungal toxins, heavy metals, salts, herbicides, low temperatures, and freezing. But only in a few instances did the selected character—expressed in cell culture or even in regenerated plants—become expressed under field conditions or was stably inherited. Thus, although this technique can be used to select and propagate mutant cells and even tolerant plants, these are probably epigenetic, that is, brought about by changes in gene expression, and unstable. However, for vegetatively propagated species or seed-propagated apomicts, this strategy has much to recommend it.

Haploids

Since its establishment by Guha and Maheshwari (1966), artificial production of haploid plants from the in vitro development of pollen grains (androgenesis) has received widespread attention for many forages. The process involves growing anthers or free microspores on an artificial medium, transferring calli that develop on the anthers' surface to a regeneration medium, and establishing the new plants.

The plants produced are generally haploid; they require doubling of the chromosome number before they become fertile and can be used in breeding programs. In *Lolium*, however, we have found that about 75% of the plants produced have a diploid complement. This raises the question of whether their origin is from microspores or from anther wall material. By applying genetic markers, we have confirmed that they are indeed derived from pollen (M. D. Hayward et al., unpublished data).

Anther culture has allowed the production of homozygous individuals for use in further breeding programs. In forage grass breeding, however, its utility has been somewhat restricted by several factors. For example, many species, such as *Brachiaria*, are recalcitrant, and have not responded to culture (J. W. Miles, 1994, personal communication). In these cases, the failure to identify responsive genotypes may be the problem, because the ability to regenerate has been clearly shown to be under genetic control in all species examined, for example, barley, wheat, rice, maize, ryegrass, and potato (Foroughi-Wehr and Wenzel, 1993). The occurrence of albino plants among regenerants is common in the anther culture of monocotyledons. Procedures for green plant production have been well established in such species as *Lolium perenne*, and have revealed the extensive variation that may be released by this method from these outbreeding species. In practice, however, we have found that the variation is not distributed in the regular Mendelian manner expected: many major gene loci show highly disturbed segregations (Hayward et al., 1990).

Because many forage species are polyploid, reducing the chromosome number does not necessarily lead to the desired homozygosity of the genome. In these species, anther culture may well have a role to play in revealing variation that would otherwise remain concealed. This could be particularly useful in apomictic species, such as those of *Brachiaria*, where a reduced chromosome complement may lead to the production of sexual, as opposed to apomictic, forms. The apomictic trait appears to be controlled by a single dominant allele in the simplex state (C. B. do Valle, 1994, personal communication). Sexual diploids derived from anther culture would greatly enhance the genetic diversity available at the diploid level in *Brachiaria*. Such material would be extremely useful in genetic mapping. Furthermore, examination of the reproductive mode of an array of random diploid genotypes derived by anther culture from apomictic tetraploid *Brachiaria* could shed light on the relationship between expression of apomixis and ploidy level.

The breeding system may further influence the use of doubled haploid forage grasses, in that many species of genera such as *Lolium* and *Festuca* have a genetically controlled incompatibility system that still functions in the homozygous state. This prevents the multiplication of superior individuals by selfing, but can be useful for producing F_1 hybrids (Hayward, 1988). One further problem, however, is the high incidence of male sterility, as we have found in our doubled haploid *L. perenne*.

Gene Transfer by Nonsexual Means

Genetic transformation and somatic hybridization provide two methods of nonsexual gene transfer. The major difference between conventional plant breeding and genetic transformation is that conventional breeding is concerned with the transfer of large numbers of genes whose characteristics are only known through phenotypic measurements. In contrast, genetic transformation manipulates small numbers of genes with high precision. Somatic hybridization also involves transfer of whole or partial genomes, but advances in molecular biology now provide more efficient means of handling large numbers of genes and of linking phenotype with genotype.

Genetic transformation

Genetic transformation can be defined as the transfer of foreign genes isolated from plants, viruses, bacteria, or animals into a new genetic background. In plants, successful genetic transformation requires the production of normal, fertile plants that express the newly inserted genes. Transformation can use gametophytic tissues prior to fertilization or somatic cells, such as explants, cells, and protoplasts, which can be stimulated to regenerate plants *de novo* in culture. In the latter case, such techniques must be available, not only for the species in question, but also for the specific cultivars, genotypes, and tissue.

Since 1980, there has been a dramatic development in the transformation of dicotyledonous species, mainly because of the application of *Agrobacterium tumefaciens* and *A. rhizogenes* as natural vectors. However, until as recently as 1988, applications to monocotyledons seemed remote, and, despite much effort in many laboratories, genetic transformation of the major cereal and grass crops—which are recalcitrant to *Agrobacterium* transformation—has been slow.

This has led to the development of direct DNA delivery techniques, such as chemical and electrical transfer of DNA to protoplasts, and microprojectile bombardment of cells and tissues with DNA-coated particles. When combined with efficient methods of regenerating plants from cell cultures and protoplasts, transformation can be successfully applied to cereals and grasses.

The process of genetic transformation involves several distinct stages: insertion, integration, expression, and inheritance of the new DNA. Methods of gene insertion can involve the use of bacterial or viral vectors and direct gene transfer. These techniques use similar gene constructs, comprising bacterial or viral promoters linked to appropriate genes. Both vector and direct gene transfer have their part to play in the transformation of monocotyledonous and dicotyledonous species, and the method chosen is generally governed by the plant species and its regenerative response in tissue culture. A suite of as many as three genes is normally inserted into the host plant's cell. The genes are a selectable gene, such as the genes governing resistance to antibiotics, a marker gene for the rapid detection of transformed cells, and the particular experimental gene under investigation. The antibiotic resistance genes permit efficient selection of transformed cells, which then divide and regenerate callus, and, ultimately, shoots and plants in the presence of the antibiotic.

Direct gene transfer to protoplasts. Isolated protoplasts were first used to demonstrate gene transfer to plant cells by determining transient expression of an introduced gene. Since then, methods developed for direct gene transfer to dicotyledonous protoplasts have been applied to monocotyledons, and have led to the successful stable integration of the introduced DNA and regeneration of transformed plants. Transgenic plants of wheat, rice, barley, orchard grass, tall fescue, and *Agrostis* have now been obtained by this method (Asano and Ugaki, 1994; Biswas et al., 1994; Horn et al., 1988; Lazzeri et al., 1991; Marsan et al., 1993; Wang et al., 1992), and we have recently demonstrated transformation of apomictic *Dichanthium annulatum* protoplasts (P. Morris et al., unpublished data).

The naturally low permeability of the plasmalemma to macromolecules must be increased to allow DNA to cross the membrane. Two methods exist for direct gene transfer to protoplasts: one relies on chemical treatment of protoplasts with polyethylene glycol (PEG) at high pH in the presence of divalent cations; the other modifies membrane structure and permeability by application of high voltages, that is, electroporation of protoplasts.

Each method has its own advantages and disadvantages, and the method

chosen will depend on the particular applications and species. Provided efficient promoters are used, direct gene transfer to protoplasts can easily be achieved. Transformation may occur at a frequency as low as 1×10^{-4}; thus the critical part of this method is the selection of the transformed protoplasts and their regeneration to give fertile plants. We have found that, provided several criteria are met (Table 1), successful plant regeneration from grass protoplasts can be achieved at a sufficiently high frequency to recover transformed plants.

Direct gene transfer to cells by microprojectile bombardment. Microprojectile bombardment involves accelerating microprojectiles (typically, tungsten or gold particles, 1-2 μm in diameter) to velocities at which they can penetrate plant cell walls. This is achieved either electrostatically or with blank cartridges in a modified firing mechanism; however, recently developed methods that use compressed air to accelerate the particles allow better control of velocity. The DNA is bound to the particles and is therefore delivered into the cell. Firing is usually carried out under vacuum, and shock-wave damage to the cell is minimized by involving an expansion chamber in the design of the machine. Critical factors in increasing transformation frequencies include the number and velocity of the microprojectiles, the type of support used for the cells or tissues, and the concentration of spermidine and $CaCl_2$ used to bind the DNA to the particles.

Detailed studies have been carried out on a wide variety of species and tissues (Potrykus, 1993). In combination with the β-glucuronidase reporter gene (*gus*), which allows the visualization of transformed cells that are transiently expressing the gene, this method of direct DNA transfer provides a powerful tool for studying gene expression in a variety of cell types, including embryogenic cell clusters; leaf epidermis and mesophyll; and cells of intact tissues, such as apical meristems and somatic and zygotic embryos. The application of this technique has permitted rapid analysis of 5' promoter regions for enhancer and silencer elements, the effect of introns, and the effect of 3' terminator regions on gene expression and mRNA stability. When used for gene transfer to intact tissue, these techniques also allow rapid analysis of tissue-specific expression of gene constructs. Such analysis is needed to ensure normal regulation of gene expression before production of transgenic plants.

Table 1. Criteria for plant regeneration from grass protoplasts.

Criterion	Remarks
Responsive genotypes	In temperate grasses, 30%-40% of genotypes give embryogenic cultures, and 60%-70% of these cultures give green plant regeneration
Highly embryogenic cell suspension cultures with high growth rate	Young cultures, derived directly from meristems or embryos or via primary callus, give high rates of plant regeneration. Frequent subculture of suspensions (7 days) and use of young cells (2-4 days after subculture) is critical
Protoplast isolation from all cell types in culture	Optimization of isolation methods to maximize number of protoplasts from embryogenic cells is essential
Culture conditions optimized for division of protoplasts from embryogenic cells	Medium osmolarity, carbon source, and plating method are particularly critical
Culture conditions optimized for embryo induction, maturation, germination, and growth of plants	As determined for the first two criteria

Recent evidence indicates that microprojectile bombardment gives results similar to DNA transfer via electroporation of protoplasts, but, without selection, will almost certainly give rise to chimeric plants. Within the grasses, microprojectile bombardment has been successfully used to obtain transformed plants of *L. multiflorum* (S. J. Dalton, 1994, personal communication), *L. perenne, Festuca pratense*, and *F. rubra* (Spangenberg et al., 1994), and we have recently demonstrated high levels of transient expression of the *gus* gene in callus cultures of apomictic genotypes of *D. annulatum* (P. Morris et al., unpublished data).

Promoters and other regulatory DNA sequences. For expression in plant cells, foreign genes need to have appropriate promoter, 5' leader, and 3' terminator sequences to ensure efficient transcription, stability, and translation of mRNA. The most common of these is the promoter of the 35S RNA gene of the cauliflower mosaic virus (CaMV). This promoter is active in all tissues, but its activity differs between cell types. It is now the most widely used constitutive promoter for transformation of dicotyledons, giving 10 to 40 times the levels of expression than either the 19S CaMV or the nopaline synthase (*nos*) promoter from *A. tumefaciens*. However, growing evidence that the 35S promoter functions less efficiently in monocotyledonous cells (at least 10 to 100 times less) than in dicotyledonous ones has led to the use of more efficient constitutive plant promoters, such as from the maize *Adh* gene, the rice *actin* gene, or the rice *ubiquitin* gene, and the use of introns immediately in front of the promoter, which dramatically increases expression in monocotyledonous cells.

Selection of transformed cells. A key factor in developing successful methods for genetic transformation is the efficacy of selection agents. First, they must be toxic to plant cells, though not so toxic that products from the dying nontransformed cells kill adjacent transformed cells. Thus, the most effective toxins are those that either inhibit growth or slowly kill the nontransformed cells; optimal selection pressure will use the lowest level of toxin needed to kill nontransformed tissues. Second, careful timing of the selection pressure is critical to limit the number of nontransformed cells that survive through cross-protection by transformed cells. Genes conferring resistance to a variety of toxic compounds, such as antibiotics and herbicides, have been fused to suitable plant promoters and used to select and identify transformed cells (Hauptmann et al., 1988). Comparisons of these different selection agents under the control of different promoters has allowed optimal systems to be developed for many species (Bowen, 1993).

Transient expression of genes and stable integration. The expression of a foreign gene by transformed plant cells can best be assessed by determining the abundance or activity of its product. The coding sequences of genes for bacterial enzymes, which are easily assayed and whose activity is not normally found in plants, form the basis of many reporter genes. Commonly used enzymes include chloramphenicol acetyltransferase (CAT), bacterial or firefly luciferase (LUX) and β-glucuronidase (GUS). These reporter genes (either as transcriptional or, more rarely, translational fusions) have been used extensively to analyze the function of promoters and other gene regulatory sequences; their availability has greatly increased the usefulness of transient assays.

The majority of the DNA introduced into cells by direct gene transfer is degraded, and only a small fraction becomes integrated with the genome. However, this DNA can be expressed in the cell and forms the basis of these transient assays. Transient expression studies require an efficient method of delivering DNA into the cells and a simple assay for the gene product. For example, protoplasts treated with DNA under suitable uptake conditions are incubated

for a time (usually 24-72 hours) to allow transcription and translation of the reporter gene. The activity of the gene product is then determined either chemically, by extraction of the protoplasts, or histochemically, with suitable substrates that yield a visible product. Histochemical assays are particularly useful for determining the frequency and type of cells that receive and express the introduced DNA. Transient assays may also be used to optimize variables associated with different methods of direct gene transfer.

In many systems, transient expression of novel genes in cells has allowed refinement of the methods of insertion, but ultimately, stable integration of the DNA into the plant's genome is required. The continued expression and stability of the novel DNA in succeeding generations is also essential, particularly in sexually reproducing crops.

One major disadvantage of direct gene transfer is the variable pattern of DNA integration that can occur. Vector DNA may be subjected to cleavage, resulting in rearrangement, truncation, tandem formation, and linkage of cotransformed genes, either before or during integration. These modifications have frequently been observed to occur at higher rates than with *Agrobacterium*-mediated transformation. Unequivocal integration of DNA into the nuclear genome, but not into the plastid or mitochondrial genomes, has been demonstrated, using the majority of direct DNA transfer methods. Several copies of genes have been shown to occur at one site, but this site differs in different transformation events (Czernilofsky et al., 1986a; 1986b). Evidence for directed integration into a predetermined location in the plant genome by homologous recombination is also leading to the development of gene targeting systems in plants (Paszkowski et al., 1988).

The method of DNA transfer may also influence the initial copy number and arrangement of the introduced DNA in the genome. The size of plasmid constructs that can be efficiently introduced by direct transfer is limited in some cases by the method of delivery. Several researchers (e.g., Krens et al., 1982) have used PEG-mediated delivery of Ti-plasmids to protoplasts, with demonstrable incorporation of the 20-kb T-DNA region, although most workers use plasmids of 5-15 kb. Shearing of DNA may limit the size of plasmid that can be transferred with the DNA gun, although plasmids of up to 16 kb have been transferred by this method (Draper et al., 1982). Thus, while 5- to 6-kb regions have been introduced into plant cells by several techniques without internal rearrangements, the delivery of intact DNA sequences greater than 16-20 kb into the plant genome is not yet possible with any reliability. However, this would be highly desirable, particularly for application of gene complementation techniques, in which DNA from genomic libraries could be used to complement, and hence identify, mutated genes.

Cotransformation with direct DNA transfer methods has also been demonstrated. *Escherichia coli* plasmid-based vectors, carrying different genes and mixed before DNA transfer methods were applied, have resulted in cell colonies containing both genes (Goto et al., 1993). Efficient cotransformation of selectable (*nptII*) and nonselectable (*gus*) genes, both under the control of the CaMV35S promoter, has been demonstrated, as has coexpression in regenerated plants (Lyznik et al., 1989).

Criteria initially used to demonstrate stable transformation—such as resistance to antibiotics or herbicides, or phenotypic changes in the plant resulting from the expression of particular genes—proved inadequate. The minimum proof of stable transformation must be the demonstration that the cell DNA contains an integrated copy (or several copies) of the introduced gene sequence. This sequence must be stably maintained during cell division, and its heritability in a Mendelian fashion should be demonstrated. Expression of the

transferred gene via determination of appropriate mRNA, protein, or enzyme activity would provide additional verification. Thus, to confirm integration, southern hybridization of genomic DNA to probes derived from regions of inserted sequence should be carried out. A useful, recent modification of this technique is the use of synthetic oligonucleotide primers, either for internal coding regions of the gene or for promoter regions (if different promoters are used and need to be distinguished). PCR can also be used to confirm the presence of the introduced sequence or sequences in the genomic DNA.

The potential of genetic transformation depends fundamentally on the existence of a very limited number of genes (preferably one), having a significant effect on a trait of economic interest. In *Brachiaria*, aside from apomixis, some forage quality, disease resistance, and developmental attributes may be amenable to genetic improvement through transformation.

Somatic hybridization

Somatic hybridization provides a further method for nonsexual gene transfer, bypassing sexual barriers to combine entire genomes. Because there are no initial barriers to protoplast fusion, species that would normally not be capable of cross-hybridization can form heterokaryons at the protoplast level. Following fusion, protoplasts containing nuclei of the parent species in common cytoplasm can be induced to regenerate a new cell wall and enter division where nuclear fusion, with or without chromosome elimination, takes place to form a somatic hybrid cell. Selection and plant regeneration from these somatic hybrids may then be possible. However, until recently, this final stage has been the main limitation to the exploitation of this technology in breeding programs.

Initially, fusion of isolated protoplasts was achieved by chemical means, using high concentrations of PEG at high pH in the presence of Ca^{++} ions, but new methods based on electrofusion have largely replaced these chemical methods. Protoplasts are fused electrically by bringing them into contact in an alternating electric field between two electrodes and fusing their plasmalemma membranes with a short (microsecond) DC pulse of 500-1,500 V/cm.

Whatever the method of fusion, efficient selection protocols are required to separate self-fusion products from interspecific hybrids and multiple fusion products. This has been achieved mechanically, by selection, with subsequent culture of individual hybrid cells; chemically, if one parent carries a resistance gene to an antibiotic or a herbicide; or by complementation between the two partners. Alternatively, when a high frequency of single-fusion hybrids is obtained, some workers have chosen bulk plant regeneration, followed by selection of somatic hybrids at the plant level. This method, however, relies on using adequate biochemical or molecular markers to identify nuclear and cytoplasmic genes unique to each parent.

Early difficulties with unstable genomes that resulted in massive chromosome elimination in symmetric somatic hybrids led to the development of asymmetric hybridization, where the donor protoplasts are irradiated and used as a source of chromosomes or chromosome fragments and fused with recipient protoplasts that have a high capacity for plant regeneration. Protoplast fusion and regeneration also facilitate the transfer of cytoplasmic genetic elements, such as mitochondria and chloroplasts, by the formation of cybrids, where the nuclear genome of the donor protoplasts is inactivated and fused with recipient protoplasts with either active or inactivated cytoplasmic genomes.

Protoplast fusion has conceptual, although as yet unproven, potential in *Brachiaria*, where distantly related species, such as *B. humidicola* and *B. decumbens*, have complementary desirable attributes that cannot be combined by conventional hybridization.

Devising Cheap and Easy Screens

Until the recent developments in molecular genetics allowed the identification of individual genes, forage breeders had very few major genes to work with, the majority of agronomically important traits being quantitative and controlled by large numbers of genes. Nowadays, a multiplicity of molecular-based techniques can be used to recognize either individual genes controlling specific biochemical or physiological characteristics, or blocks of genes controlling quantitative traits (quantitative trait loci, or QTLs). A knowledge of the action and interaction of these individual genes can be most useful in breeding programs, for example, to identify cultivars or individual genotypes, provide potential pathways, and introduce or modify specific physiological traits.

Genetic fingerprinting

The ability to identify individual cultivars, populations, or genotypes is becoming increasingly important in forage breeding. As Plant Breeders' Rights are more widely adopted, cultivars must be unequivocally identified for registration purposes. The characterization of germplasm collections dictates that specific reproducible measures of genetic diversity, free of environmental influences, be employed. Breeders often have a requirement in their crossing programs to identify the provenance of individuals. This is particularly true in possible apomictic species, such as *Brachiaria*, where progenies must be differentiated as either sexual or apomictic. Several procedures, including biochemical or molecular markers, are applicable to these problems. The well-known isozyme methods are relatively easy to apply and inexpensive. Although Hayward and McAdam first proposed their use for this purpose in 1977, these methods are only now becoming accepted as a means of distinguishing cultivars of forage grasses. However, they have been more widely accepted for characterizing germplasm (Pérez de la Vega, 1993) and for identifying hybrids or sexual progenies from apomicts, for example, in *Brachiaria* by Hacker (1988) and Calderón and Agudelo Cortés (1990). But the lack of variability at the controlling loci limits the use of isozymes, and we need to use certain DNA techniques for enhanced discrimination.

Many forage grass genomes contain large proportions of repetitive DNA sequences, some of which can be characterized as variable number tandem repeats (VNTRs), or minisatellites, or as the simpler sequence repeats, known as microsatellites (Weising et al., 1994). The number of repeating mini- or microsatellite units can vary considerably in a particular DNA sequence and throughout the genome, with variation being detectable down to the individual. This variability can be revealed by differential electrophoretic mobility of DNA fragments containing different numbers of repeated sequences produced by digestion with restriction enzymes. These differences can be visualized by using the mini- or microsatellite sequences themselves as probes. We have recently identified some putative sequences in *Lolium*, which hold promise for fingerprinting purposes (M. D. Hayward et al., unpublished data).

Genetic mapping with molecular markers

The construction of detailed genetic linkage maps for many crop species has been revolutionized by the development of methods for detecting polymorphisms at the molecular level. Because these methods are relatively inexpensive, plant breeders are finding them increasingly practical (Tanksley et al., 1989). These molecular polymorphisms can be characterized as detectable changes in either protein or DNA sequences. The most commonly used classes of DNA polymorphisms used in genetic mapping are those detected as restriction fragment length polymorphisms (RFLPs) or those

based on the use of the PCR, such as random amplified polymorphic DNAs (RAPDs) or amplified fragment length polymorphisms (AFLPs) (for further details, see Pérez de la Vega, 1993). Application of one or more of these techniques to an appropriate segregating population, such as an F_2, backcross, or recombinant line (e.g., doubled haploids), can lead to the construction of genetic maps. In ryegrass, we have used, as a mapping family, a test cross of an interspecific hybrid between *L. perenne* x *L. multiflorum* crossed to a doubled haploid *L. perenne*. To date, we have identified seven major linkage groups, with a total map length of 550 centimorgans. We could allocate two groups to specific chromosomes, thanks to earlier work that had used trisomic addition lines and had placed two specific isozyme marker loci on to separate chromosomes (Figure 4).

Marker-assisted selection

Marker-assisted selection has become possible because genetic linkage maps can be generated from molecular markers with a wide coverage of the genome (Tanksley et al., 1989). If a molecular marker can be shown to be linked to a desired phenotypic trait, then, at an early stage of a breeding program, individual plants carrying that marker and, by association, the linked genes controlling the desired trait can often be selected. The advantage of this scheme over traditional approaches is that the gene or genes controlling the phenotypic character can be selected, even in the absence of its phenotypic expression, thus minimizing developmental or

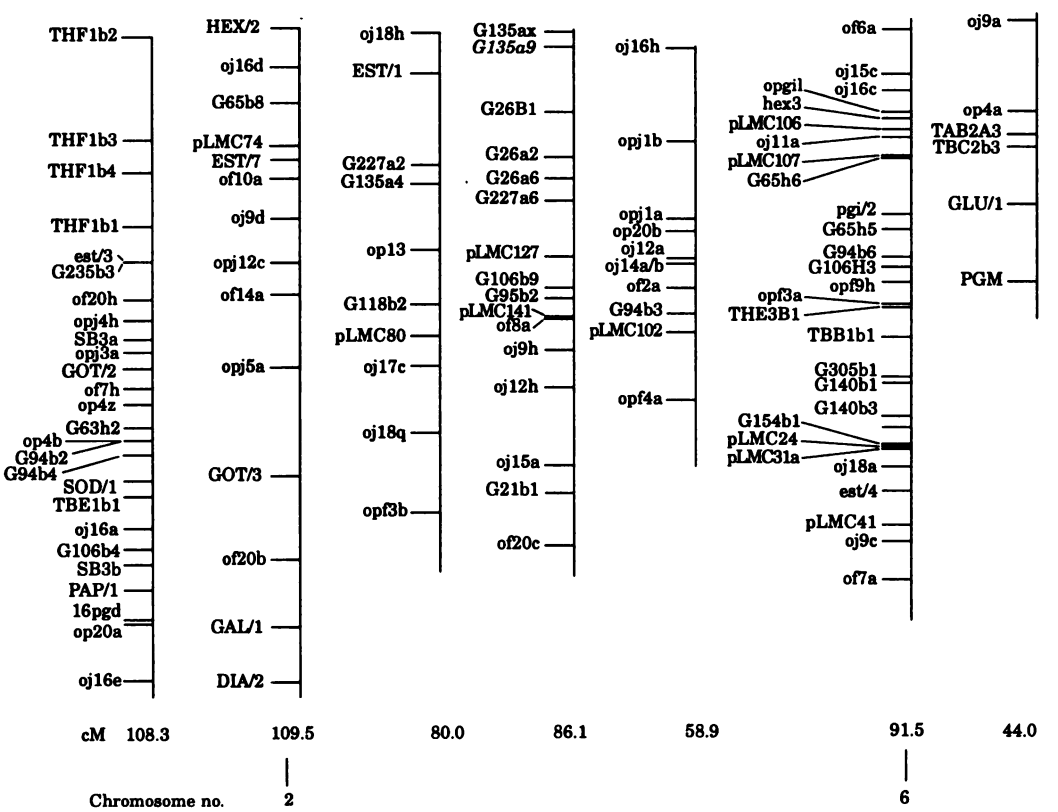

Figure 4. Linkage groups in *Lolium*.

environmental impact on the selection procedure. This scheme may also allow a greater selection intensity if, for example, screening is done at the seedling stage, when many more individuals can be handled.

Molecular markers can be used to assist selection either for single genes of major effect, such as the gene in *Brachiaria* controlling reproductive mode, or for QTLs. The main limitation is the degree of linkage between the gene or genes of interest and the flanking markers. The tighter these linkages are, the smaller the probability of recombination between the gene(s) of interest and the flanking markers; thus, the more accurate the predictive ability of marker-assisted selection. In ryegrass, for example, our genetic map enabled us to locate several significant QTLs, such as those controlling some phenological processes and quality traits (Hayward et al., 1994).

Progress has been made in marking the apomixis locus in *Brachiaria* (Tohme et al., Ch. 13, this volume). Current markers, however, are not sufficiently tightly linked for good prediction and routine use in breeding programs.

Cytological localization of genes

For many genetic mapping programs, allocating linkage groups to specific chromosomes is not necessary. But where a breeding program involves introgression of genes by interspecific or intergeneric hybridization into an otherwise agronomically acceptable cultivar, the breeder often needs to establish where and to what extent recombination has taken place, thus ensuring the full fertility of the derived material. Recently developed techniques from in situ hybridization (ISH) can now precisely identify introgressed genes (Thomas et al., 1994).

In in situ hybridization, a specific region of a chromosome can be visualized directly by using fluorescently labeled DNA probes (FISH) that will hybridize only to homologous regions of the genome. When used with an in situ DNA amplification technique (primed in situ labeling, or PRINS), the sensitivity can be such that a single gene position can be identified (Craig et al., 1992). Thus, when used in conjunction with phenotypic assessment, in situ hybridization can identify the chromosomal location of a particular gene introgressed into an alien genome, or of a transgene introduced by genetic transformation. The former is exemplified by the location by Thomas et al. (1994) of the chromosomal segment carrying a gene controlling the senescence processes in backcross progenies of *L. perenne* x *F. pratensis*.

Manipulation of Plant Processes

Genetic manipulation requires the definition of physiological, morphological, and biochemical objectives, as well as the identification and cloning of the relevant agronomically important genes. The precise characterization of particular agronomic traits, at the gene product level, is therefore essential to the successful use of genetic manipulation. However, many important agronomic characters, such as persistence or yield, cannot be easily defined in terms of single-gene products. At present, therefore, traits controlled by single Mendelian genes have the best chances for successful manipulation. The trait produced by genetic transformation will be novel and a dominant trait. This simplifies selection and shortens breeding times, compared with conventional breeding procedures. It also eliminates the difficulties encountered in dealing with recessive characters.

Several types of genes can be isolated and used to manipulate plant processes. These range from genes that code for proteins or enzymes as desirable end products (such as proteins of pharmaceutical interest or industrial enzymes) to genes for enzymes that divert

biochemical pathways in more favorable directions, homeotic regulatory genes, and the promoter and enhancer regions that direct cell or organelle specificity or show environmental or chemical induction.

Several strategies exist to manipulate genes, that is, to increase or decrease gene expression. One technique of down-regulating the expression of a gene, using antisense RNA, has been successfully used to modify several plant processes of agricultural significance, including ripening in tomato (Hall et al., 1993); secondary metabolism (flower color in *Petunia*: Mol et al., 1989); lignification in tobacco (Dwivedi et al., 1994; Halpin et al., 1994); tannin biosynthesis in *Lotus corniculatus* (Carron et al., 1994); and carbon partitioning in potato (Spychalla et al., 1994). Recent developments in sense expression of genes include modifications to the protein quality in white clover (Ealing et al., 1994); numerous examples of protection against viral diseases by the expression of viral coat proteins; resistance to insects by expression of the *Bacillus thuringiensis (Bt)* gene (Fujimoto et al., 1993; Koziel et al., 1993); and the introduction of resistance to herbicides (Murray et al., 1993).

Conclusions

Biotechnology clearly offers today's breeder opportunities that were little more than pipe dreams to the pioneers of forage breeding. Novel variation can be released from existing genomes. New combinations of entire genomes can be created by bringing together a multiplicity of genes. Genetic markers now available not only allow the effective manipulation of this novel variation, but also contribute to more traditional breeding procedures by increasing selection efficiency and identifying cultivars for registration purposes. Individual genes can now be moved across species barriers, even from bacteria and animals into plants.

The employment of these various methods, however, must still be subjected to decisions proposed at the outset. Only by developing an integrated approach to breeding that embraces both the breeder and the biotechnologist can we expect to make the most effective use of these new tools. In addition, we must also be mindful of the need to maintain existing germplasm stocks as reservoirs of genes to exploit in these procedures, and to consider the wider implications of introducing some of these novel sources of variation into species that are still major components of natural ecosystems.

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Chapter 13

Applications of Biotechnology to *Brachiaria*

J. Tohme, N. Palacios, S. Lenis, and W. Roca*

Abstract

Advanced biotechniques offer the potential for greater precision and efficiency in genetic manipulation of crop species. Applications of molecular markers in *Brachiaria* include assessment of genetic variation, gene tagging, and genetic mapping. In particular, recent applications of molecular-marking techniques to apomixis provided strong evidence of single-gene inheritance of reproductive mode in *Brachiaria*. Regeneration protocols for *Brachiaria* have been worked out and plants of four *Brachiaria* species have been regenerated. These tools provide a basis for a project aimed at fine-mapping the apomixis gene, and its possible cloning and transfer to other crop species.

Introduction

Biotechnology is now widely recognized as a powerful tool for helping agricultural researchers use genetic resources better, select desirable genotypes efficiently, speed up crop breeding, and introduce novel genes from sources inaccessible to conventional sexual hybridization. By enabling the detailed analysis of genetic structure of plants and associated microorganisms, biotechnological tools will help develop higher yielding and more stable genotypes.

In this chapter, we will illustrate the application of biotechnology tools to *Brachiaria* improvement at CIAT: using molecular markers to study genetic similarity among selected *Brachiaria* species, tagging the apomixis gene, and tissue culture techniques to establish regeneration protocols.

Molecular Markers

Molecular markers are DNA sequences that allow differentiation among genotypes at the DNA level. They can be genes or DNA segments with no known or coding function but whose inheritance can be followed easily by using well-established laboratory procedures (for a comprehensive review, see Paterson et al., 1992). The DNA markers most commonly used to detect DNA polymorphism are based on the restriction fragment length polymorphism (RFLP) technique (Botstein et al., 1980; Burr et al., 1988) and on the random amplified polymorphic DNA (RAPD) assay based on the polymerase chain reaction (PCR) (Williams et al., 1990). The RFLP technique detects polymorphism in the length of fragments of DNA digested with restriction enzymes, and hybridization with either random genomic or complementary DNA (cDNA) probes. The technique is usually slow and labor intensive.

The RAPD markers are PCR-based and are generated by amplifying genomic DNA, using a single primer of arbitrary base sequence; these markers detect nucleotide sequence polymorphism either at the primer annealing sites or in the region being amplified. The RAPD assays are fast, easy to use, require only a small amount of DNA, and are more amenable to automation than RFLPs (Table 1). While each method has its advantages and disadvantages, molecular markers such as RFLPs and PCR-based RAPDs, sequence characterized amplified regions

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Table 1. Characteristics of molecular markers for gene tagging.

Characteristic	RFLPs[a]	RAPDs[b]	SCARs[c]	Primers flanking microsatellite
Assay	Restriction, blotting	PCR[d]	PCR	PCR
Detection	Hybridization	DNA staining	DNA staining	DNA staining
Inheritance	Codominant	Dominant	Dominant, codominant	Codominant
DNA required	2-10 µg	10-50 ng	10-50 ng	10-50 ng
Locus detected	1-3	1-10	1	1
Polymorphism	Low-medium	Medium	Medium	High
Robotics	Difficult	Possible	Possible	Possible

a. RFLP = restriction fragment length polymorphism.

b. RAPD = random amplified polymorphic DNA.

c. SCAR = sequence characterized amplified region.

d. PCR = polymerase chain reaction.

(SCARs), and microsatellites have become extensively used as tools in the genome-wide examination of plant chromosomes.

Molecular markers have been used to address research topics related to phylogenetic relationships (Kochert et al., 1991; Miller and Tanksley, 1990), gene flow (Doebley, 1990), characterization of gene pools and estimation of genetic diversity (Dweikat et al., 1993; Wang and Tanksley, 1989), genome mapping and gene tagging of important agronomic traits (McCouch et al., 1988; Tanksley et al., 1989), and study of quantitative trait loci (QTL) (Lander and Botstein, 1989).

Uses of RAPD Markers to Determine Genetic Relationships

CIAT holds one of the world's largest collections of tropical forage germplasm, including a large collection of *Brachiaria*, of which about 85% was assembled through a collecting mission to East Africa during 1984/85 (Keller-Grein et al., Ch. 2, this volume). The accessions are being characterized for edaphic adaptation (Rao et al., Ch. 4, this volume), reaction to key pests and diseases (Valério et al., Ch. 6, this volume), as well as for other attributes. Because most of the polyploid biotypes are apomicts, genetic improvement of *Brachiaria* depended on the identification, collection, and preservation of existing natural variation. Only when a fertile tetraploid was developed from the sexual diploid *B. ruziziensis*, could breeding begin to improve species such as *B. decumbens* and *B. brizantha* (Miles and Valle, Ch. 11, this volume; Valle and Savidan, Ch. 10, this volume).

Considering the nature of *Brachiaria*'s mode of reproduction, an understanding of the genetic relationships between and within species will contribute to designing better strategies for collecting and conservation. It will also provide breeders with adequate information on the genetic base being used and allow rational selection of parents to maximize the expression of heterosis.

In describing genetic relationships, the approaches previously available have used data of comparative morphology, physiology, and isozymes (Keller-Grein et al., Ch. 2, this volume; Renvoize et al., Ch. 1, this volume). More recently, several molecular techniques for detecting polymorphism at the DNA level have been applied; DNA markers such as RFLPs or PCR-based RAPDs are being used extensively for determining genetic relationships (Debener et al., 1990; Devos and Gale, 1992; Furnier et al., 1990; Halward et al., 1992; Lanham et al., 1992; Tingey and Tufo, 1993).

We have begun studying *Brachiaria* species through PCR-based RAPD markers. Applied to studies of genetic

relationships, this technique involves screening DNA for scrabble polymorphism, using a series of 10-base-pair primers of arbitrary sequence to amplify random anonymous DNA fragments. The method typically yields polymorphism with dominance-recessive characteristics.

Genetic relationships among *Brachiaria* species were compared, using RAPD primers (Suárez, 1994). The genotypes evaluated included 58 accessions of *B. decumbens*, *B. brizantha*, *B. ruziziensis*, *B. jubata*, *B. humidicola*, and true *B. dictyoneura*, which are of major interest to forage programs in tropical America and represent a diverse range of germplasm, both for ploidy level and for agronomic characteristics. The RAPD data were generated by amplifying total DNA, using random 10-base nucleotide sequences as primers in PCR reactions. These data were analyzed by principal component analysis (PCA) and cluster analysis, applying the unweighted pair-group method arithmetic average (UPGMA). The grouping pattern obtained (Figure 1) is consistent with assigning *B. decumbens*, *B. brizantha*, and *B. ruziziensis* to one taxonomic group, and *B. jubata*, *B. humidicola*, and true *B. dictyoneura* to another (Renvoize et al., Ch. 1, this volume). This preliminary survey points to areas for further investigation:

1. The relationship between *B. decumbens* and *B. ruziziensis*. Based on our RAPD data, all sexual and some other accessions of *B. decumbens* are closely similar to *B. ruziziensis* accessions.

2. The amount of diversity present in sexual versus apomictic species. The sexual *B. ruziziensis* displayed less variability than the apomictic species *B. decumbens* and *B. brizantha*.

This preliminary survey shows the usefulness of PCR-based markers, such as RAPDs, for discriminating among different species from the *Brachiaria* germplasm collection and for differentiating genotypes within species. We are pursuing this genetic characterization to understand the amount of diversity present in the collection and to obtain more information about the distribution of diversity in relation to the reproductive mode of the genotypes.

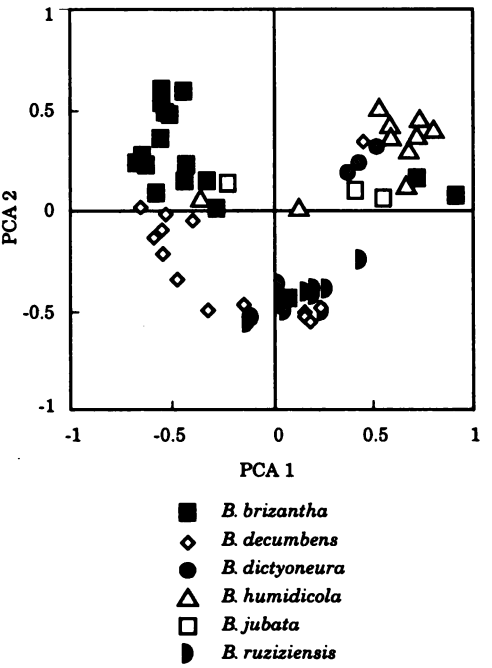

Figure 1. Genetic similarity of six *Brachiaria* species determined by using principal component analysis (PCA) on RAPDs data. (After Suárez, 1994.)

Toward the Construction of a *Brachiaria* Molecular Map

Advances in genetic mapping tools have greatly simplified and extended genetic studies to a large number of organisms (Botstein et al., 1980). Before the introduction of molecular approaches, comprehensive genetic maps were available only for very few species. Generating the data necessary to construct genetic maps of morphological markers was laborious and usually involved only a few loci. A molecular

genetic map represents the relative location of clearly identifiable molecular markers such as RFLPs and RAPDs. By correlating the inheritance of such markers with agronomic traits, it will be possible to identify the location of important genes, allowing the indirect selection for a specific trait without having to wait for its phenotypic expression. Use of DNA markers linked to traits of interest will permit prediction of mature plant attributes at the seedling stage, facilitating early selection and the development of novel and more efficient breeding strategies.

Molecular maps developed for various species have allowed greater understanding of the genetics of the species, gene tagging of important agronomic traits (Tanksley et al., 1989), and the study of complex QTLs (Lande and Thompson, 1990; Lander and Botstein, 1989; Melchinger, 1990; Paterson et al., 1990; Soller and Beckmann, 1990). Maps have been constructed for both diploid (e.g., rice: McCouch et al., 1988; diploid *Solanum*: Bonierbale et al., 1988) and polyploid (e.g., sugarcane: Al-Janabi et al., 1993) species.

A genetic map of *Brachiaria* can be constructed, based on segregation of RFLP or RAPD markers in an F_1 population derived from two heterozygous parental clones. This will provide several genome-wide markers to monitor introgression of useful traits from different species of *Brachiaria* into commercially acceptable germplasm and facilitate breeding of complex traits. We have begun to construct a *Brachiaria* map, using RAPD primers obtained commercially and heterologous RFLP probes from the rice (McCouch et al., 1988) and maize maps (probes from the University of Missouri-CIMMYT: Coe et al., 1990). Recent studies on comparative mapping have revealed significant conservation among several crop species in the Gramineae (Ahn and Tanksley, 1993; Ahn et al., 1993; Hulbert et al., 1990; Melake Berhan et al., 1993). These findings suggest that if homology is detected between *Brachiaria* and other Gramineae, genetic information and probes from rice, maize, and sorghum can be used, thus accelerating the mapping of *Brachiaria*.

Preliminary screening indicates good homology between rice and *Brachiaria*. Such comparative mapping will (1) accelerate the construction of a *Brachiaria* map; (2) provide a better understanding of the evolution of the Gramineae genome; and (3) facilitate the cloning of genes by providing access to DNA libraries and technology already available in well-mapped species, such as rice or maize.

Tagging the Apomixis Gene

Molecular markers provide an efficient means of locating and monitoring genes of agronomic importance; RAPD markers have been shown to be effective in gene tagging in tomato (Martin et al., 1991), lettuce (Michelmore et al., 1991), and *Arabidopsis* (Reiter et al., 1992). A major target trait for gene tagging in *Brachiaria* is the apomixis gene. The common commercial species, *B. decumbens* and *B. brizantha*, are tetraploid apomicts. They are cross-compatible with an induced tetraploid *B. ruziziensis* that is sexual (Ndikumana, 1985; Swenne et al., 1981). Apomixis appears to be controlled by a single dominant gene (Valle and Glienke, 1993; J. W. Miles and J. Tohme, unpublished data). The reproductive mode of individuals in segregating progenies can be determined by microscopic observation of the structure of embryo sacs in cleared ovaries (Valle et al., 1991; Young et al., 1979; Valle and Savidan, Ch. 10, this volume) or, less reliably, by progeny testing (Miles and Valle, 1991). However, both methods are time-consuming and tedious. A molecular genetic marker closely linked to the apomixis gene, which would permit identification of reproductive mode of small seedlings, would greatly improve the efficiency of *Brachiaria* breeding. The

identification of such a marker is a necessary first step to mapping of the apomixis gene and its eventual cloning and transfer into other crop species.

We have used the RAPD technique to tag the apomixis gene. This method, combined with bulk segregant analysis (Michelmore et al., 1991), allows the quick screening of a large number of markers to detect markers linked to the target trait.

DNA was bulked from apomictic or sexual F_1 individuals from a cross involving a sexual tetraploid *B. ruziziensis* clone and an apomictic *B. brizantha* accession. Parental genotypes are assumed to be highly heterozygous. Samples of DNA from each parent and from each of the two F_1 bulks were amplified, using random 10-mer oligonucleotide primers (Figure 2). Putative markers linked to the apomixis gene were identified by screening a large F_1 population from the same cross. Because of the number of copies per RAPD (2-5), questions are raised as to the reproducibility of the technique in a different genetic background. A method for using SCARs—PCR-based markers that represent a single genetically defined locus—was proposed to address this limitation of RAPDs (Paran and Michelmore, 1993). This technique

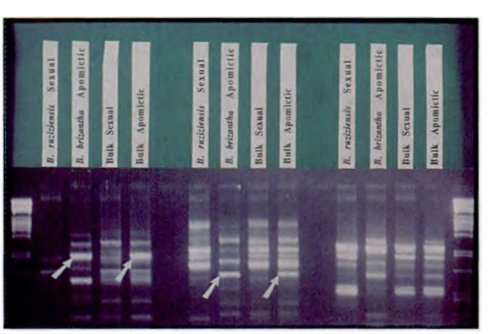

Figure 2. Amplification of genomic DNA obtained from sexual *B. ruziziensis* or apomictic *B. brizantha* parental genotypes, or bulked from apomictic or sexual hybrid progeny genotypes. The arrows point to fragments present in the apomictic parent and apomictic bulk, but absent in the sexual parent and sexual bulk.

complements RAPD markers; as it detects only a single locus, amplification is less sensitive to reaction conditions, and SCARs can potentially be converted into codominant markers.

SCARs are obtained from the specific amplification of the DNA with base-pair primers designed from the sequence of only the RAPD fragment that cosegregates with the trait of interest. To generate SCARs, the RAPD reaction is performed, using the normal PCR protocol. On the average, five bands are obtained from each primer. For the cloned RAPD amplification product, two oligonucleotides are designed to be used as SCARs primers. Each primer contains the original 10 bases of the RAPD primer plus the next 14 internal bases from the end. We are currently generating the fine mapping of the apomixis gene, using RFLP probes and the newly developed technique of amplified fragment length polymorphism (AFLP) (Hayward et al., Ch. 12, this volume).

Regeneration of *Brachiaria* Species

Genetic engineering of any species requires efficient regeneration and transformation protocols; such protocols for *Brachiaria* are essential, should cloning of the apomixis gene be contemplated. To date, most tissue culture research with forage grasses has been conducted with temperate species. Efficient in vitro protocols have been developed for plant regeneration via somatic embryogenesis (Lu and Vasil, 1982; 1985; Wang and Vasil, 1982). We report here the first successful regeneration of genotypes of *B. brizantha*, *B. decumbens*, *B. ruziziensis*, and *B. dictyoneura* CIAT 6133 (S. Lenis and W. Roca, unpublished data).

Freshly harvested, mature seed of each line was surface-sterilized and placed on callus induction media, using a modification of the protocol developed for rice (Takamizo et al., 1990). The most

effective auxin for callus growth was 2,4-dichlorophenoxy-acetic acid (2,4-D), and the best results were obtained with 2 mg/L. Presence of casein hydrolysate, along with 2,4-D in the medium, resulted in higher callus induction, as in other crops (Takamizo et al., 1990; Torello et al., 1984; Wang and Yan, 1984).

After 2 to 4 weeks of culture, growth of two types of callus were observed on the seed explants: a compact, whitish translucent callus, originated from the scutellum of seeds, which eventually gave rise to embryogenic tissue; and a friable, nonembryogenic callus. Embryogenic callus was separated from friable callus before transfer to regeneration medium (Figure 3).

For regeneration, potentially embryogenic calli were transferred to MS salts (Murashige and Skoog, 1962) supplemented with vitamins (Gamborg et al., 1976), myoinositol, α-naphthylacetic acid (NAA), kinetine, 3% sucrose, and 0.6% agar. Cultures were maintained at 28 °C in the dark during callus induction or in a 12-hour photoperiod (2,500 lux illumination) during regeneration.

Embryogenic callus developed in 1 to 2 weeks of culture in the regeneration medium. To obtain further differentiation of embryos and subsequent shoot development, it was necessary to transfer the embryogenic calli to fresh regeneration medium; shoot regeneration occurred 2 to 4 weeks later (Figure 4).

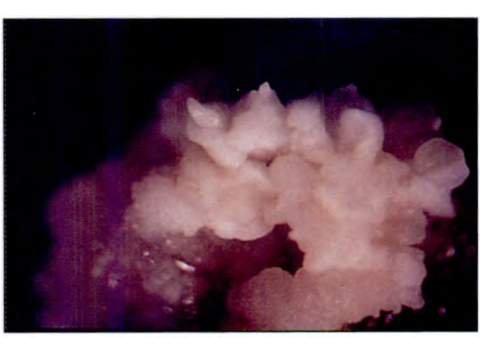

Figure 3. Embryogenic callus formation of *Brachiaria*.

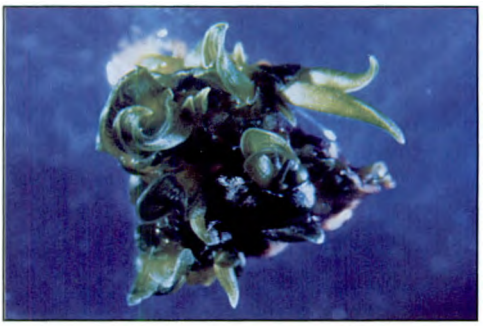

Figure 4. Shoot regeneration of *Brachiaria* after the transfer of embryogenic calli to a fresh regeneration medium.

After 3 to 4 weeks under the regeneration conditions, young shoots were transplanted into sterilized soil in the greenhouse. Similar reports of somatic embryogenesis in Gramineae have described the initiation of coleoptile, coleorhiza, and scutellum (Chen et al., 1985; Vasil and Vasil, 1981a; 1981b). Our studies suggested that plant regeneration is of embryogenic origin, as found in several Gramineae (Lu and Vasil, 1982; 1985; Wang and Vasil, 1982).

Conclusion

All existing *Brachiaria* cultivars, based directly on introduced wild germplasm, have agronomic limitations (Keller-Grein et al., Ch. 2, this volume). Molecular markers and tissue culture techniques provide tools to increase the effectiveness of genetic improvement of *Brachiaria*. Future application will no doubt concentrate on fine mapping of the apomixis gene, the construction of the map (an essential step to tagging and dissecting complex traits, such as spittlebug resistance), and a transformation system. As the tagging of the apomixis gene and the construction of a molecular map progress, it will be feasible to contemplate cloning the apomixis gene. Several key elements for this task are available, making it possible to consider *Brachiaria* as an additional plant model for cloning the apomixis gene and understanding its mechanisms.

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Chapter 14

Regional Experience with *Brachiaria*: Tropical America—Humid Lowlands

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Abstract

Brachiaria species have become important components of sown pastures in the humid lowlands of tropical America. This ecosystem occupies about 50% of Brazil; 60% of the area encompassed by Bolivia, Peru, and Ecuador; 14% of Mexico; and significant areas in other countries of the region. The cultivars most commonly evaluated across sites are *B. decumbens* cv. Basilisk, *B. brizantha* cv. Marandu, *B. humidicola* cv. Humidícola, and *B. dictyoneura* cv. Llanero.

Cultivar Basilisk is the most widely used in the region, because it adapts to a wide range of soils and is easy to manage and to establish from seed. However, it is highly susceptible to spittlebugs and is associated with photosensitization in cattle. Cultivar Marandu is resistant to spittlebugs, but requires soils of medium to high fertility and does not tolerate waterlogged sites. Cultivars Llanero and Humidícola are better adapted to poorly drained soils, but have only medium to low nutritional quality. Soil compaction, spittlebug infestation, and runoff of soil nutrients are factors associated with *Brachiaria* pasture degradation in the humid tropics; however, few studies report on pasture reclamation.

During the last 15 years, part of the large germplasm collection maintained at CIAT has been evaluated in the American humid tropics. Promising new accessions of *Brachiaria* have been identified as potentially productive, but more research is needed on their seed production, pest and disease tolerance, compatibility with legumes, persistence, and animal productivity.

Introduction

The tropical American humid lowlands

Of the 1,514 million hectares in the American tropics, a large proportion is occupied by humid lowlands. By using total wet-season potential evapotranspiration (WSPE), number of rainy months, and wet-season mean temperature (WSMT), Cochrane et al. (1985) divided the humid tropics into two major subecosystems: (1) the tropical rain forest (TRF), with a WSPE of >1,300 mm, >9 rainy months, and a WSMT of >23.5 °C; and (2) the tropical semievergreen seasonal forest (TSSF), with a WSPE of 1,061-1,300 mm, 8-9 rainy months, and a WSMT of >23.5 °C. Usually, the TSSF lies along the fringes of the rain forest and has a distinct wet and dry period (Sharma et al., 1992), whereas the TRF usually has no distinct dry period.

The predominant soils in the tropical American humid lowlands are acidic Oxisols and Ultisols (pH = 3.8-5.5), with high Al concentration (>60%) and low P content and interchangeable bases (Sánchez and Isbell, 1979). Other less acidic and more fertile soils in this region, particularly in Central America and Mexico, are Inceptisols (young acid soils), Entisols, Alfisols, Mollisols, and Vertisols. The main nutrient limitations of these

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soils, especially of Oxisols and Ultisols, relate to P, K, and Ca deficiencies (CIAT, 1983; Cochrane et al., 1985).

The TRF and TSSF subecosystems occupy about 50% of Brazil (Serrão et al., 1990); 60% of the area encompassed by Peru, Bolivia, and Ecuador; and are important in Panama (48%), Colombia (37%), Costa Rica (35%), Honduras (29%), and Mexico (14%) (RIEPT, 1987).

Brachiaria in the tropical American humid lowlands

Cattle farming in the humid lowlands of tropical America is based on cultivated pastures planted on acid and low- to medium-fertility soils, mainly Oxisols, Ultisols, and Inceptisols. *Brachiaria* species of African origin have adapted well to this ecosystem, and several commercial cultivars have been released in the last 30 years.

Important environmental factors affecting the adaptation and productivity of *Brachiaria* pastures—particularly of *B. decumbens* cv. Basilisk and *B. humidicola* cv. Humidícola—are altitude, soil pH, soil P content, and pests and diseases. Despite its susceptibility to spittlebugs, cv. Basilisk continues to be widely used by farmers in the humid tropics, because it adapts to a wide range of edaphic conditions, is highly stoloniferous, easy to establish from seed, resistant to leafcutting ants, and responsive to good management.

Large germplasm collections of *Brachiaria* species are available now at institutions such as CIAT and EMBRAPA, and are being characterized and evaluated to identify superior ecotypes (Keller-Grein et al., Ch. 2, this volume). During the last 15 years, adaptation trials have been carried out from southern Mexico to the humid tropics of Bolivia.

In this chapter, we review the experience gained with *Brachiaria* species in the tropical American humid lowlands—particularly the present status of germplasm evaluation—alone and in association with legumes, animal productivity, seed production, and problems associated with pasture degradation and reclamation.

Germplasm Evaluation

Although several species of *Brachiaria* are native to the American continent (Sendulsky, 1978; Renvoize et al., Ch. 1, this volume), all the economically important species have been introduced from Africa: in early colonial times, *B. mutica* (paragrass) (Parsons, 1972), and, between the 1950s and 1970s, *B. decumbens*, *B. brizantha*, *B. ruziziensis*, and *B. humidicola*. Currently, the largest ex situ germplasm collection of *Brachiaria* is maintained at CIAT, Cali, Colombia (Keller-Grein et al., Ch. 2, this volume). Part of it has been evaluated at major screening sites in Peru, Costa Rica, and Brazil through CIAT's Tropical Forages Program and selected accessions have been evaluated in regional trials of the International Tropical Pasture Evaluation Network (RIEPT, its Spanish acronym) (Pizarro et al., Ch. 15, this volume).

Evaluation at major screening sites

Major germplasm collections of *Brachiaria* species have been or are being evaluated at six locations in the humid lowlands; Table 1 shows the soil type, rainfall, and predominant ecosystem at each site. The largest collection, comprising 208 accessions, was evaluated at Pucallpa, Peru, on an acid Ultisol between 1988 and 1991 (G. Keller-Grein, unpublished data). Another large collection (203 accessions) was evaluated at Guápiles, Costa Rica, on a moderately acid, medium-fertility Inceptisol (Table 1) (CIAT, 1993; Vallejos et al., 1989; P. J. Argel, unpublished data). At both sites, DM yields, pests and diseases, and other agronomic parameters were recorded.

Peru. The collection at Pucallpa included accessions of *B. brizantha* (41%) and *B. decumbens*, *B. humidicola*, *B. jubata*, and *B. ruziziensis*, which together

Table 1. Characteristics of six sites used to evaluate *Brachiaria* germplasm in the tropical American humid lowlands.

Country	Site	Predominant ecosystem[a]	Rainfall		Soil			
			mm/year	Dry months per year (no.)	Type	pH	Al sat. (%)	P (ppm)
Panama	Gualaca	TRF	4000	3-4	Inceptisol	4.7	21.0	3.5
Costa Rica	Guápiles	TRF	4300	0	Inceptisol	5.5	2.2	8.3
Bolivia	Chipiriri	TRF	4670	0	Inceptisol	5.1	80.0	14.0
Colombia	Caquetá	TRF	3600	1	Ultisol	4.5	62.0	5.7
Peru	Pucallpa	TSSF	2048	2	Ultisol	4.4	81.0	2.0
Brazil	Paragominas	TSSF	1774	5	Oxisol	5.5	0	1.3

a. TRF = tropical rain forest; TSSF = tropical semievergreen seasonal forest.

made up another 53%. Intraspecific variation was particularly large for *B. brizantha*. Most of its accessions gave high DM yields during both the wet and dry seasons. The accessions CIAT 16098, 16113, 16127, 16130, 16143, 16158, 16305, 16306, 16318, and 16320 outyielded the commercial check, cv. Marandu.

Most accessions of *B. humidicola* gave relatively low DM yields, but had high proportions of leaf DM and good soil cover. Similarly, a large proportion of *B. decumbens* had a short growth habit and gave low DM yields; several accessions had better yields but no one was superior to the control, cv. Basilisk. Most accessions of *B. jubata* and *B. ruziziensis* were characterized by a semierect growth habit and intermediate yields. While most *B. jubata* accessions performed well, accessions of *B. ruziziensis* exhibited chlorosis, indicating poor adaptation to the edaphic conditions. Twenty-eight promising accessions were selected for further evaluation.

Costa Rica. The germplasm evaluated at Guápiles consisted of *B. brizantha* (101 accessions), *B. humidicola* (36), *B. decumbens* (29), *B. jubata* (16), *B. ruziziensis* (14), *B. arrecta* (3), *B. dictyoneura*[1] (2), *B. platynota* (1), and *B. bovonei* (1). Soil cover, plant height, and DM yields were measured at 8-week intervals over 2 years. As at Pucallpa, considerable differences were observed between and within species. Cluster analysis of the agronomic data yielded seven contrasting groups (Table 2).

The group with tall species, good soil cover, and high DM yields (cluster 3) included *B. brizantha* CIAT 667 and CIAT 26110, and *B. decumbens* CIAT 16497. Another outstanding group (cluster 2) consisted of *B. decumbens* cv. Basilisk, *B. brizantha* CIAT 16300 and CIAT 16305, *B. ruziziensis* CIAT 26170 and CIAT 26175, and *B. humidicola* CIAT 26407.

Cultivars Marandu, La Libertad (CIAT 26646), Humidícola, and Llanero, and *B. dictyoneura* CIAT 16510 grouped in cluster 6, which gave good soil cover but had medium plant height and intermediate DM yields. Most of the accessions of *B. arrecta* and *B. jubata* were in cluster 7, a group with acceptable soil cover, but short plants and low DM yields.

Screening for spittlebug resistance at Pucallpa or Guápiles was not possible because the pest occurred only occasionally during the period of evaluation. However, moderate incidence of *Cercospora* and foliar blight caused by *Rhizoctonia solani* was recorded at Guápiles, particularly on accessions of *B. brizantha* and *B. ruziziensis*. Rust caused by *Uromyces setariae-italicae* was

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Table 2. Classification of 203 accessions of *Brachiaria* species by cluster analysis of dry matter yield (DMY), soil cover, and plant height at Guápiles, Costa Rica.

Cluster	Number of accessions	DMY (kg/ha)		Soil cover (%)		Plant height (cm)		Species and accessions†
		Mean‡	Range	Mean‡	Range	Mean‡	Range	
1	11	1444 g	1194-1618	62 d	40-90	40 e	26-61	*B. brizantha* (4); *B. jubata* (5); *B. decumbens* (2)
2	6	4669 b	4592-4770	93 a	84-100	61 ab	51-70	*B. decumbens* cv. Basilisk; *B. brizantha* (2); *B. ruziziensis* (2); *B. humidicola* CIAT 26407
3	3	5042 a	4958-5148	96 a	92-99	67 a	57-82	*B. brizantha* CIAT 667, CIAT 26110; *B. decumbens* CIAT 16497
4	52	3149 d	2857-3419	88 ab	67-99	52 bcd	31-74	*B. brizantha* (29); *B. decumbens* (8); *B. humidicola* (10); *B. humidicola*; *B. ruziziensis* (5)
5	58	2553 e	2282-2847	84 bc	64-97	49 cde	24-88	*B. brizantha* (32); *B. jubata* (4); *B. decumbens* (7); *B. ruziziensis* (4); *B. arrecta* CIAT 16844; *B. humidicola* (10); *B. decumbens*
6	26	3673 c	3424-4164	90 ab	82-99	55 bc	41-85	*B. brizantha* cvs. La Libertad and Marandu + (14); *B. humidicola* cv. Humidícola + (5); *B. ruziziensis* CIAT 26174; *B. decumbens* CIAT 26182; *B. dictyoneura* CIAT 16510 and cv. Llanero
7	47	1992 f	1670-2230	80 c	49-97	43 de	24-65	*B. brizantha* (16); *B. humidicola* (11); *B. decumbens* (10); *B. jubata* (6); *B. arrecta* (2); *B. ruziziensis* (2); *B. humidicola*

† Values in parentheses indicate number of accessions.

‡ Means followed by the same letter are not significantly different ($P < .05$), according to Duncan's Multiple Range Test.

SOURCE: P. J. Argel, unpublished data.

moderate on *B. humidicola* accessions (except for CIAT 26149, which showed good resistance to the fungus) and on cv. Llanero.

Twenty promising accessions were initially selected at Guápiles. These were further tested for adaptation on an infertile acid Ultisol, where their number was narrowed down to 10 accessions: *B. brizantha* CIAT 6387, 16168, 16322, 16549, 16827, 16835, and 26110; *B. decumbens* CIAT 16497; and *B. humidicola* CIAT 16886 and CIAT 26149.

These elite materials are currently being evaluated at Guápiles for tolerance of waterlogging. Preliminary observations show that *B. brizantha* CIAT 16827 and 16835, and cvs. Marandu and La Libertad have lost vigor, and some plants have died 7 months after planting in a site of high water saturation. A second group—formed by *B. brizantha* CIAT 26110,

16322, 16168, and 6387, and *B. decumbens* CIAT 16497 and cv. Basilisk—has also lost vigor but has shown no plant mortality. In contrast, *B. humidicola* accessions CIAT 26149 and 16886, and cvs. Humidícola and Llanero are vigorous and not affected, even by a permanently high water table (P. J. Argel, unpublished data).

Colombia. Based on selections made in Pucallpa, Peru, and Carimagua, Colombia, 58 accessions from seven species have been agronomically evaluated during 1993-1995 in the Andean piedmont near Florencia, Caquetá, Colombia (B. L. Maass, G. Keller-Grein, and C. G. Meléndez, unpublished data). Accessions of *B. brizantha*, *B. decumbens*, and *B. humidicola* were particularly well adapted, producing vigorously during the bimonthly cutting regime. Spittlebug incidence was relatively low and only few accessions were severely damaged, whereas strong incidence of foliar blight caused by *Rhizoctonia solani* was recorded for 35 accessions, especially during the rainy season. Eleven of the best performing accessions have been selected for further testing under grazing in association with *Arachis pintoi*.

Brazil. Forty-two accessions of *B. brizantha*, *B. decumbens*, *B. humidicola*, and *B. ruziziensis* have been evaluated at Paragominas, Pará, Brazil (Dias Filho et al., 1990). The most promising accessions proved to be *B. brizantha* BRA-004219, BRA-003441 (= CIAT 16315), and BRA-004308 (= CIAT 26110); *B. decumbens* BRA-004391; and *B. humidicola* BRA-005126.

Other sites in the tropical lowlands. Adaptation trials with 21 to 36 accessions of *Brachiaria* have also been carried out at other sites in the American humid tropics, such as Chipiriri in Bolivia (Ferrufino and Vallejos, 1986), Gualaca in Panama (Urriola et al., 1988), San Martín in Peru (Valles, 1985), and several sites in the humid tropics of southern Mexico (Peralta, 1986). Seasonal DM yields and tolerance of drought, pests, and diseases have been recorded. Although direct comparisons are not possible because of differences in the methodology used, results indicated that, at Chipiriri, *B. ruziziensis* CIAT 6134, 6130, and 6241, and *B. decumbens* cv. Basilisk, CIAT 6370, 6700, 6012, and 6132 were highly susceptible to the spittlebugs *Aeneolamia astralis*, and *Zulia* and *Mahanarva* species. Similarly, at San Martín, accessions of *B. ruziziensis* and *B. brizantha* CIAT 6016 and CIAT 667 were highly susceptible to *Zulia pubescens*, and species of *Tomapsis*, *Aeneolamia*, and *Deois*.

Accessions of *B. humidicola* (CIAT 6705, 6709, 6369, 682, and cv. Humidícola) adapted well to the acid Inceptisols and the 4-month dry period at Gualaca. However, at the same site, accessions of *B. decumbens* (CIAT 6131, 664, and 6132) and *B. ruziziensis* CIAT 654 were highly susceptible to foliar blight. Across sites, cv. Llanero showed good adaptation and acceptable tolerance of pests and diseases.

Boddey and Victoria reported (1986) a capacity in various *Brachiaria* species for biological nitrogen fixation (BNF), which may explain their ready adaptation to the humid tropics. By using ^{15}N-labeling techniques, these authors demonstrated that BNF accounted for 39.1% (45 kg/ha) of the total N accumulated by *B. decumbens* IRI 700; 29.6% (29 kg/ha) of that accumulated by *B. humidicola* IRI 409 (CIAT 6013); and 9.6% (9.8 kg/ha) of that accumulated by *B. ruziziensis* cv. Kennedy. These findings should be investigated further, and BNF capacity perhaps used as a selection criterion for screening new accessions of *Brachiaria* (Boddey et al., Ch. 5, this volume).

Regional evaluation

The data generated by RIEPT cover the area from southern Mexico to northern Bolivia, the evaluation sites representing most of the soil and climatic variation found in the American humid tropics. A total of 47 accessions of eight *Brachiaria* species, mainly *B. brizantha*, have undergone regional agronomic evaluation

at various sites in the TSSF and TRF ecosystems. The methodology used was that recommended for RIEPT type B trials (Toledo and Schultze-Kraft, 1982). Seasonal dry-matter yields of this germplasm is summarized in the Appendix at the end of the chapter. The accessions most commonly evaluated across sites are *B. decumbens* CIAT 606 (cv. Basilisk), *B. brizantha* CIAT 6780 (cv. Marandu) and CIAT 6387, *B. humidicola* CIAT 679 (cv. Humidícola) and CIAT 6369, and *B. dictyoneura* CIAT 6133 (cv. Llanero).

The RIEPT database contains data for cv. Humidícola at 23 evaluation sites and for cv. Basilisk at 39 sites. Stepwise multiple regression analysis of agronomic attributes on environmental variables showed that, in the tropical American humid lowlands, altitude and soil pH are the major determinants of adaptation of cv. Humidícola; whereas, for cv. Basilisk, soil P level also had major effects on adaptation (Table 3). These factors, however, accounted for only 50% of the observed variability for dry matter (DM) yields, soil cover, or dry-to-wet season growth ratios (RGI). Thus, other factors (e.g., incidence of pests and diseases) influenced the adaptation of these *Brachiaria* cultivars, although to a lesser degree.

The RIEPT database enabled comparisons of DM yield, soil cover, and plant height in cvs. Marandu, Llanero, and Basilisk for 21 of the locations where they were evaluated. Cultivars Marandu and Basilisk had similar plant cover and height 12 weeks after planting, and similar DM yields and RGI ratios 12 weeks after cutting. Cultivar Llanero was shorter, slower to cover the soil, and yielded less DM during both maximum and minimum rainfall periods. In the TSSF of Mexico, Central America, and the Caribbean, cv. Llanero produced yields comparable with those of the other two cultivars, but was less productive during the minimum rainfall period in the TRF ecosystem.

Table 3. Influence of altitude, phosphorus (P), and soil acidity on plant cover 12 weeks after planting, dry matter yield (DMY), and relative growth index (RGI) of two *Brachiaria* cultivars at 12-week regrowths during periods of maximum (max) and minimum (min) rainfall in several localities of the American humid tropics.

Species, cultivar (accession)	Group[a]	Number of localities	Altitude (m.a.s.l.)	P (ppm)	pH (1:1)	Cover at 12 weeks after planting (%)	DMY (kg/ha)		RGI[b]
							Max	Min	
B. humidicola	1	3	13	NS[c]	7.3	64	9,583	1,767	0.2
cv. Humidícola	2	11	155	NS[c]	4.8	47	–3,352	2,442	0.7
(CIAT 679)	3	8	1,420	NS[c]	5.0	50	–6,635	5,031	0.8
	4	1	1,295	NS[c]	4.0	82	4,250	2,474	0.6
		(23)							
B. decumbens	1	3	13	4.5	7.3	40	7,871	2,816	0.4
cv. Basilisk	2	21	162	2.8	5.1	61	–4,764	4,251	0.9
(CIAT 606)	3	6	703	11.5	4.7	76	–5,952	3,766	0.6
	4	9	1,228	4.0	4.9	57	–11,934	7,104	0.6
		(39)							

a. Through cluster analyses, based on the most important environmental factors determined by stepwise multiple regression analyses, for each species four environmental groups were formed that explained 93% and 66% of the variability observed on *B. humidicola* and *B. decumbens*, respectively.

b. RGI was calculated as follows: DMY min/DMY max.

c. P did not significantly effect the adaptation of *B. humidicola* cv. Humidícola.

SOURCE: G. Keller-Grein, P. J. Argel, L. H. Franco, and G. Ramírez, unpublished data.

Commercial Cultivars

Despite the large number of evaluations done on germplasm collections of *Brachiaria* species during the last 15 years across the tropical American humid lowlands, the commercial cultivars available to farmers are still limited to cvs. Basilisk, Humidícola, Marandu, La Libertad, and Llanero, the traditional paragrass (*B. mutica*), tannergrass (*B. arrecta*), and ruzigrass (*B. ruziziensis*). Also, but recently, available is brachipará, an apparent natural hybrid of *B. plantaginea* with *B. mutica* (C. B. do Valle, 1994, personal communication). However, published information on its adaptation or animal performance does not exist.

The commercial cultivars are adapted in different degrees to the soils and climates of the tropical American humid lowlands. Even so, all current cultivars have major limitations, particularly susceptibility to spittlebugs and problems related to edaphic adaptation and seed quality (Keller-Grein et al., Ch. 2, this volume).

Germplasm potentially more productive than the commercial cultivars is undoubtedly available in the collections. However, most of the evaluations have only characterized the agronomic adaptation of the new *Brachiaria* accessions and have not documented other factors that would determine their value in cultivated pastures, such as persistence and animal productivity.

Brachiaria decumbens cv. Basilisk

Cultivar Basilisk, a vigorous, stoloniferous perennial grass, is one of the most widely used pasture grasses in the American humid tropics, although few new plantings have been reported during the last decade in the Brazilian Amazon because of its high susceptibility to spittlebugs (Dias Filho, 1987). Once established, this cultivar can tolerate, temporarily, waterlogged soils, although it does better on well-drained ones. Cattle graze this grass readily, although horses do not.

Establishment and maintenance. Pastures of cv. Basilisk are usually established by seed, either broadcast or planted in rows (Gil et al., 1991). However, successful vegetative plantings are also reported in the humid tropics (Botero B. and Cardozo, 1994). In Panama, Hertentains et al. (1992) found that selected vegetative material established more rapidly when spot-planted at 50 x 50 cm than when planted in rows 75 cm apart. In the humid tropics of Panama and Costa Rica, nursery plots are often established from seed on small farms, then transplanted as 1-month-old seedlings to the field (L. Hertentains, 1994, personal communication). This method reduces loss of seed, and as soil moisture in the field is good, transplanting seedlings is safer than other methods.

Pastures are not usually fertilized in the tropical American humid lowlands; however, cv. Basilisk has responded to increasing levels of N in the acid Ultisols of Pucallpa, with DM yield increasing from 9 t/ha with 0 N to 19 t/ha with 800 kg/ha of N (Ara and Toledo, 1979). Similar observations were reported by Vallejos (1986) from Valle del Sacta in Bolivia, and by Amaya Hernández and Meléndez Nava (1988) from the acid savannas of Tabasco in Mexico.

Cultivar Basilisk has also responded to P fertilization. At Huimanguillo (Mexico), Pastrana (1994) studied the effect of P sources on DM yields of cv. Basilisk and found that maximum yields were obtained with 80 kg/ha rock phosphate or 100 kg/ha triple superphosphate. At Pucallpa, the strongest response was observed with 40 kg/ha of P (Ara and Toledo, 1979).

Compatibility with legumes. In the American humid lowlands, cv. Basilisk is almost exclusively planted as a monocrop, although, in Colombia, compatibility was reported with the

following legumes: *Desmodium ovalifolium* CIAT 350 (cv. Itabela) and *Centrosema macrocarpum* CIAT 5713 on the acid Ultisols of Quilichao (Giraldo and Toledo, 1985; Rodríguez et al., 1991); *Pueraria phaseoloides* (tropical kudzu) in Villavicencio (Pérez B., 1985); and *Arachis pintoi* CIAT 17434 (cv. Mani Forrajero) in the TRF of Caquetá (Gil et al., 1991). A small area of cv. Basilisk associated with tropical legumes is also found in the Brazilian Amazon (Serrão et al., 1990). However, this grass is normally aggressive, competing strongly with associated legumes over the long run.

Disadvantages. As a pasture grass for the humid tropics, cv. Basilisk has two drawbacks. It has been associated with skin photosensitization in cattle, a serious problem in young animals (Lascano and Euclides, Ch. 7, this volume). It is also highly susceptible to spittlebugs (Valério et al., Ch. 6, this volume), although the degree of plant mortality varies according to region. It is worse in South America than, for instance, in Central America, perhaps because of differences in spittlebug species. In contrast, the grass tolerates leaf-eating insects, such as *Spodoptera* sp. (Valério et al., Ch. 6, this volume).

Brachiaria humidicola cv. Humidícola

Cultivar Humidícola is a stoloniferous grass that tolerates waterlogged or intermittently flooded soils such as chromic Vertisols (Amaya Hernández and Carmona Muñoz, 1988). Although it can withstand dry periods (Gonçalves et al., 1987; Teixeira Neto and Veiga, 1987; Urriola et al., 1988), DM yields may be reduced by as much as 40% (Tergas, 1981). On infertile Ultisols, it has responded to P fertilization (Souza Filho and Dutra, 1991) and, at Chiapas, to 80 kg/ha N and 120 kg/ha P (Amaya Hernández, 1988).

Establishment and maintenance. Although this cultivar can be propagated from seed, in the humid tropics, farmers usually favor vegetative propagation with mature stolons, because seed is either not readily available or is of unreliable quality. The grass is slow to cover the soil, but once established, it competes aggressively with weeds (a major problem in pastures of the humid tropics) and reduces soil erosion.

This cultivar produces high DM yields (Dias Filho, 1983) but is regarded as a low- to medium-quality forage (Lascano and Euclides, Ch. 7, this volume). Its in vitro dry matter digestibility (IVDMD) ranges from 48% to 62%, and crude protein (CP) from 5% to 12% (Hoyos and Lascano, 1985; Muñoz M., 1985), although N fertilization improves these quality parameters (Botrel et al., 1990). Levels of Ca and P are about 0.34% and 0.13%, respectively (Abaunza et al., 1991).

Compatibility with legumes. Because of its strongly stoloniferous growth habit, cv. Humidícola is reputedly difficult to associate with tropical legumes. However, productive and stable associations have been reported with *D. ovalifolium* CIAT 350 in Yurimaguas, Peru (Alegre and Lara, 1991; Reátegui et al., 1985); in Macagual, Colombia (Maldonado and Velásquez, 1990); and in Itabela, Brazil (Santana et al., 1993). Cultivar Humidícola also associates well with *A. pintoi* (Gil et al., 1991). Other less persistent associations have been reported with *C. macrocarpum* CIAT 5062, *C. brasilianum* CIAT 5234, *Calopogonium mucunoides* (Costa et al., 1991), and *P. phaseoloides* (Pérez B., 1985).

Disadvantages. Cultivar Humidícola tolerates spittlebugs, but is not truly resistant, and can therefore suffer severe damage during spittlebug outbreaks (Lapointe and Miles, 1992). The degree of damage depends on nymph populations, as Westin Consenza (1985) reported for the spittlebug *Deois flavopicta*. This grass also suffers severe damage from attacks of the striped grassworm, *Mocis latipes* (Muñoz M., 1985), but is highly resistant to leafcutting ants, such as *Acromyrmex*

landoltii (CIAT, 1989). Forage productivity is also affected, particularly in the Ecuadorean Amazon, by the rust-causing foliar fungus *U. setariae-italicae*, which has also been reported from Brazil, Colombia, Peru, Costa Rica, and Cuba (CIAT, 1989; [1990]; Valério et al., Ch. 6, this volume).

Brachiaria dictyoneura cv. Llanero

Cultivar Llanero was first released in Colombia and has since been released in other countries (Keller-Grein et al., Ch. 2, this volume). The grass has a semierect growth habit and adapts well to a range of well-drained soils, particularly on hillsides of the American humid tropics (Botero B. and Cardozo, 1994). It grows from 0 to 1,100 m.a.s.l.; at higher altitudes, it yields less, but the leaf-to-stem ratio is greater (Montenegro and Pinzón, 1992).

Cultivar Llanero is regarded as a medium-quality grass (slightly better than cv. Humidícola) that tolerates heavy grazing. It is not highly competitive during establishment, which favors associations with forage legumes. Thus, successful and productive associations have been reported with *C. acutifolium*, *C. macrocarpum*, *Stylosanthes guianensis*, *A. pintoi*, *P. phaseoloides*, and *D. ovalifolium* (Gil et al., 1991; Lascano and Avila, 1991; Lascano et al., 1991; Pérez B., 1985; Reátegui et al., 1990; Valero et al., 1987). However, cv. Llanero showed poor ability to compete for light when intercropped with either cowpea (*Vigna unguiculata*) or soybean (*Glycine max*) in a premontane TRF of Costa Rica (Duarte, 1991; Pérez et al., 1993): DM yields were 80% lower in association with soybean and 90% lower with cowpea than in monoculture. This was related to the slow initial growth rate of cv. Llanero and to a habit that favors lateral rather than vertical growth.

Cultivar Llanero tolerates high populations of spittlebugs. It also tolerates rust (CIAT, [1990]), but is susceptible to leafcutting ants during establishment (Lapointe and Miles, 1992). However, it regrows faster than cvs. Humidícola and Basilisk after a dry period (Valério et al., 1988).

Brachiaria brizantha cvs. Marandu and La Libertad

Two cultivars of *B. brizantha*—Marandu and La Libertad—have been available to farmers of the American humid tropics for the past 10 years. Cultivar Marandu is a highly productive grass, but requires more fertile and better-drained soils than other species of *Brachiaria*. It is resistant to rust, leafcutting ants, and spittlebugs, but is highly susceptible to Rhizoctonia foliar blight (CIAT, 1993; Urriola et al., 1988; Valério et al., Ch. 6, this volume).

Cultivar Marandu associates well with *D. ovalifolium*, *C. brasilianum*, *C. macrocarpum*, *C. mucunoides*, *P. phaseoloides*, and *A. pintoi* (CIAT, 1993; Costa et al., 1991; Ibrahim, 1994). This grass apparently competes efficiently when planted with a companion crop, for instance, Pérez et al. (1993) reported that when intercropped with soybean, it yielded 66% (251 g/plant) of the yield in monoculture (355 g/plant) in a premontane TRF of Costa Rica, suggesting shade tolerance and efficient use of light and soil nutrients.

Cultivar La Libertad adapts to less fertile soils than cv. Marandu. In Central America, it tolerates spittlebugs and resists rust (CIAT, [1990]).

Other *Brachiaria* cultivars

Besides the *Brachiaria* cultivars described, other materials have been adopted by farmers, although they have scarcely been researched or been formally released. Examples are paragrass, tannergrass, ruzigrass (sometimes commercialized as 'Acriana'), and more recently, brachipará.

All can be readily propagated by vegetative means, which probably facilitated their spread from farmer to farmer. Some, such as paragrass, can also produce viable seed (Grof, 1969).

Ruzigrass does not adapt to low-fertility or waterlogged soils, whereas paragrass, tannergrass, and brachipará adapt to heavy soils of medium to high fertility.

Evaluation under Grazing

A number of grazing experiments have evaluated persistence, compatibility with legumes, and animal productivity of several *Brachiaria* species in the American tropical humid lowlands. For instance, at Guápiles, Costa Rica, Ibrahim (1994) found high DM yields, particularly at the low stocking rate of 1.75 animal units/ha, of cv. Marandu associated with *A. pintoi*, *C. macrocarpum* CIAT 5713, or *S. guianensis* CIAT 184 (Table 4). *Arachis pintoi* persisted over 2.5 years of grazing, especially at the high stocking rate of 3.0 hd/ha. The other legumes did not persist, becoming dominated by the grass and by unpalatable volunteer species. After 4 years of grazing, the association of cv. Marandu and *A. pintoi* yielded an annual 990 kg/ha of beef—280 kg more than did the grass alone.

Pizarro (1985) compiled the results of three small-plot grazing trials in TSSF ecosystems, and Keller-Grein (1990) of nine in TRF ecosystems, conducted by RIEPT on *Brachiaria* pastures in Bolivia, Brazil, Colombia, Ecuador, and Peru. In terms of pasture productivity and stability, the most promising associations with legumes were (a) *B. humidicola* with *D. ovalifolium* CIAT 350 and a stocking rate of 2 hd/ha at the Centro de Pesquisas do Cacau (CEPEC) in Itabela, Bahia, Brazil; (b) *B. humidicola* with *D. ovalifolium* CIAT 350 or *Pueraria phaseoloides* CIAT 9900, evaluated at EMBRAPA's Unidade de Execução de Pesquisa de Ambito Estadual (UEPAE), Porto Velho, Rondônia, Brazil, and at the Instituto Veterinario de Investigaciones Tropicales y de Altura (IVITA), Pucallpa, Peru; and (c) *B. dictyoneura* CIAT 6133 with *Centrosema macrocarpum* CIAT 5735 and CIAT 5674 and stocking rate of 2 AU/ha at IVITA, Pucallpa, Peru (Keller-Grein, 1990).

In contrast, associations of *B. dictyoneura* cv. Llanero and *D. ovalifolium* CIAT 350 were less stable at Pucallpa, exhibiting a rapid increase of the legume in the pastures, regardless of stocking rate (Keller-Grein, 1990). *Brachiaria decumbens* cv. Basilisk proved to be compatible with the aggressive legume *D. ovalifolium* CIAT 350 in Quilichao, Colombia, and Chimoré, Bolivia; and, over time, dominant in association with *Zornia latifolia* CIAT 728 at Chimoré (Pizarro, 1985).

An association of *B. dictyoneura* cv. Llanero and *D. ovalifolium* CIAT 350 at Puerto Bermúdez, Peru, showed, regardless of grazing management, rapid degradation in terms of grass and legume availability, which was related to high compaction of the clay soil (Reátegui et al., 1990).

Table 4. Composition of pastures of *Brachiaria brizantha* cv. Marandu in association with legumes and grazed at two stocking rates, Guápiles, Costa Rica.

Associated legume	Low stocking rate (1.75 AU/ha)				High stocking rate (3.0 AU/ha)			
	Grass (%)	Legume (%)	Volunteer species (%)	DMY[a] (t/ha)	Grass (%)	Legume (%)	Volunteer species (%)	DMY[a] (t/ha)
+ *Arachis pintoi*	84.9	10.8	4.3	7.0	72.5	20.0	7.5	4.8
+ *Centrosema macrocarpum*	89.1	0.7	10.2	7.2	92.5	1.7	5.8	4.8
+ *Stylosanthes guianensis*	95.6	2.0	2.5	7.2	89.8	2.7	7.3	5.2

a. DMY = dry matter yield.

SOURCE: Ibrahim, 1994.

Table 5 summarizes animal liveweight gains obtained in various grazing experiments conducted in the American humid lowlands to measure productivity of *Brachiaria* pastures. In general, *Brachiaria* pastures have high carrying capacity that result in high animal production per unit area (see further discussion by Lascano and Euclides in Ch. 7, this volume).

Seed Production

The commercial *Brachiaria* cultivars flower and set seed at low latitudes in the humid tropics, but in general, seed yields are low and unreliable, varying from season to season (Hopkinson et al., Ch. 8, this volume). Reported seed yields range from 3 to 20 kg/ha for cv. Basilisk, 5 to 30 kg/ha for cv. Marandu, and 15 to 75 kg/ha for cv. Humidícola. Cultivar Llanero yields 50-250 kg/ha, but its strong seed dormancy is a problem (CIAT, 1989; [1990]; Vela et al., 1991; Hopkinson et al., Ch. 8, this volume). Seed yields can be improved with good management and N application (Carmona et al., 1988), but these increases are not always harvestable, as seed maturation in the humid tropics usually coincides with periods of rain.

Brachiaria Pasture Degradation and Reclamation

Pasture degradation is common in the tropical American humid lowlands, because of mismanagement, spittlebug outbreaks, soil compaction, and/or loss of soil nutrients, particularly P (Alvim, 1979; Serrão and Toledo, 1990; Veiga and Serrão, 1987; Boddey et al., Ch. 5, this volume). Soil compaction hampers interchange of atmospheric gases, moisture retention, and, consequently, root growth. At two sites, apparent density (AD), an indicator of soil compaction, was higher under *Brachiaria*

Table 5. Animal liveweight gains (LWG) on *Brachiaria* pastures at different sites in the American humid tropics.

Pasture	Site	Ecosystem[a]	Stocking rate (an./ha)	LWG				Reference
				Grass alone		Grass and legume		
				g/an. per day	kg/ha per year	g/an. per day	kg/ha per year	
cv. Llanero	Gualaca, Panama	TRF	4-6	360	783	-	-	Montenegro and Pinzón, 1992
cv. Llanero + *D. ovalifolium*	Quilichao, Colombia	TSSF	4	-	-	350	511	Lascano et al., 1991
cv. Humidícola	Napo, Ecuador	TRF	2	565	406	-	-	Muñoz M., 1985
cv. Humidícola + *P. phaseoloides*	Gualaca, Panama	TRF	4	318	501	380	585	Ortega and Urriola, 1988
cv. Humidícola + *D. ovalifolium*	Yurimaguas, Peru	TRF	4	-	-	430	692	Reátegui et al., 1985
cv. Basilisk + *D. ovalifolium*	Yurimaguas, Peru	TRF	4	-	-	379	640	Reátegui et al., 1985
cv. Marandu + *A. pintoi*	Guápiles, Costa Rica	TRF	4[b]	354	710	460	990	Hernández et al., 1995

[a] TRF = tropical rain forest; TSSF = tropical semievergreen seasonal forest.

[b] Animal units per hectare.

pastures than under primary or secondary forest (Alegre and Lara, 1991; Pinzón and Amézquita, 1991). In these examples, AD increased after 3 years of grazing at Yurimaguas, and, in the low terrace country of Caquetá, AD tended to be higher in lower layers of the soil profile (Table 6).

However, degraded *Brachiaria* pastures can be recovered. For instance, at Quilichao, a 9-year-old degraded pasture of cv. Basilisk was successfully regenerated by strip-planting it with the legumes *C. macrocarpum* and *C. acutifolium* (CIAT, 1989). At Porto Seguro, in Brazil, mechanical treatments (plowing, harrowing, or cultivating) had no significant effect on the recovery of degraded cv. Basilisk pastures, but the application of 22 kg/ha of P and the combination of this treatment with burning produced good results (Arruda et al., 1987). However, burning should be used with caution, because of the fragility of the humid tropical ecosystem.

Other practices suggested for reclaiming degraded cv. Basilisk pastures are planting short-cycle crops associated with legumes (Veiga and Serrão, 1987), or applying high levels of N (Ordóñez and Toledo, 1985). However, little research information is available on *Brachiaria* pasture degradation in the long term, and more studies are needed on this process (Boddey et al., Ch. 5, this volume).

Future Research Needs

Currently available commercial *Brachiaria* cultivars no doubt have merits that farmers appreciate. However, promising new *Brachiaria* ecotypes have been identified that may be superior to currently used ones. A complete evaluation of these new materials is therefore needed, with particular emphasis on persistence, animal productivity, seed production, tolerance of waterlogging, and reaction to pests and diseases.

The selection criteria currently used also need to be revised. The fact that farmers continue to sow *B. decumbens* cv. Basilisk, despite its high susceptibility to spittlebugs, indicates that they value its forage qualities. Exposing new materials as early as possible to farmers will

Table 6. Apparent density (AD) of soil under forest or *Brachiaria* pastures at two tropical rain forest sites in northwestern South America.

Site, country	Vegetation	Age (years)	Soil type	Depth (cm)	AD[a] (g/cm³)	Reference
Caquéta, Colombia	Forest	40	Typic hapleudult Isohyperthermic Fine clay loam	0-5 5-15	0.79 0.99	Pinzón and Amézquita, 1991
	B. decumbens[b] (Hilly country)	10	Typic hapleudult Isohyperthermic Fine clay loam	0-5 5-15	0.97 1.50	
	B. decumbens (Low terrace)	15	Typic distropet Isohyperthermic Fine clay loam	0-5 5-15	1.22 1.23	
Yurimaguas, Peru	*B. decumbens*/ *D. ovalifolium*	4	Typic paleudult	10	1.35	Alegre and Lara, 1991
	B. humidicola/ *D. ovalifolium*	3		10	1.44	
	Secondary forest	-		10	1.20	

a. Apparent density determined by the cylinder method.

b. Grazing was either rotational, alternate, or continuous, at different stocking rates.

contribute to the selection of new *Brachiaria* germplasm with high chances of adoption.

Sound methods or systems need to be developed for reclaiming degraded *Brachiaria* pastures. The use of forage legumes in this process should be encouraged. Also necessary are studies on pasture degradation in terms of soil compaction, loss of soil nutrients, and other associated factors.

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To save space, the following acronyms are used in place of publishers' names:

CPAC = Centro de Pesquisa Agropecuária dos Cerrados

CPATU = Centro de Pesquisa Agropecuária do Trópico Úmido

IDIAP = Instituto de Investigación Agropecuaria de Panamá

INIAA = Instituto Nacional de Investigación Agraria y Agroindustrial

INIFAP = Instituto Nacional de Investigaciones Forestales y Agropecuarias

IVITA = Instituto Veterinario de Investigaciones Tropicales y de Altura

RIEPT = Red Internacional de Evaluación de Pastos Tropicales

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Appendix. Seasonal Dry-matter Yields of *Brachiaria* Species in Tropical Forest Ecosystems During RIEPT[a] Trials.

Species	CIAT accession no. (cultivar)	Ecosystem[b]	Season[c]	Number of sites	DM yield over 12 weeks (kg/ha)	
					Mean	Range
B. brizantha	6294 (cv. Marandu)	TSSF	Min	1	1,000	
			Max	1	3,513	
		TRF	Min	3	1,687	1,332-2,080
			Max	3	2,821	1,707-4,284
	6297 (cv. Marandu)	TSSF	Min	1	1,377	
			Max	1	2,265[d]	
	6387	TSSF	Min	11	2,696	935-6,692
			Max	14	4,215	707-7,699
		TRF	Min	5	2,481	913-3,707
			Max	7	2,871	969-5,647
	6780 (cv. Marandu)	TSSF	Min	12	2,161	374-5,567
			Max	19	4,140	410-10,653
		TRF	Min	8	2,910	927-5,113
			Max	10	3,765	947-8,246
	16094	TSSF	Min	1	1,237	
			Max	1	6,608	
	16107	TSSF	Min	1	939	
			Max	1	1,133[d]	
	16121	TSSF	Min	1	955	
			Max	1	1,022	
	16135	TSSF	Min	1	1,204	
		TRF	Max	1	1,574[d]	
	16162	TSSF	Max	1	1,569	
	16168	TSSF	Min	1	1,225	
			Max	1	1,518[d]	
	16294	TSSF	Min	1	1,435	
			Max	1	1,950[d]	
	16301	TSSF	Min	1	1,268	
			Max	1	1,580[d]	
	16315	TSSF	Min	1	1,682	
			Max	1	2,758[d]	
	16318	TSSF	Min	1	1,461	
			Max	2	2,089[d]	1,639-2,539
	16319	TSSF	Min	1	1,644	
			Max	1	718[d]	
	16337	TSSF	Max	1	4,718	
	16339	TSSF	Min	1	1,041	
			Max	1	1,096[d]	
	16467	TSSF	Min	1	1,207	
			Max	1	1,821[d]	
	16473	TSSF	Min	1	1,403	
			Max	1	977[d]	
	16488	TSSF	Min	1	1,291	
			Max	1	2,017[d]	
	16827	TSSF	Min	1	1,232	
			Max	1	1,916[d]	
	26110	TSSF	Min	1	1,823	
			Max	1	2,031[d]	
	26646 (cv. La Libertad)	TSSF	Min	2	3,383	2,066-4,700
		TRF	Min	2	2,361	2,002-2,720
			Max	4	3,165	2,390-4,101

(Continued)

Appendix. (Continued.)

Species	CIAT accession no. (cultivar)	Ecosystem[b]	Season[c]	Number of sites	DM yield over 12 weeks (kg/ha)	
					Mean	Range
B. decumbens	606 (cv. Basilisk)	TSSF	Min	23	3,129	193-9,041
			Max	30	5,010	35-16,284
		TRF	Min	25	2,748	77-8,967
			Max	26	3,564	689-15,763
	664[a]	TSSF	Min	1	1,734	
			Max	1	2,617	
		TRF	Min	1	693	
			Max	1	902	
	665[a]	TSSF	Min	2	2,828	629-5,028
			Max	1	12,133	
		TRF	Min	1	2,472	
			Max	1	2,547	
	6012	TSSF	Min	1	1,033	
			Max	1	5,232	
	6699	TSSF	Min	1	1,246	
			Max	1	4,613	
	6700	TRF	Min	1	477	
			Max	1	1,192	
	16100	TSSF	Min	1	1,278	
			Max	1	4,473	
	16488	TSSF	Min	1	1,291	
			Max	1	2,017[d]	
	16500	TSSF	Min	1	1,072	
			Max	1	1,113[d]	
B. humidicola	679 (cv. Humidícola)	TSSF	Min	14	2,394	176-4,750
			Max	17	4,982	126-12,104
		TRF	Min	10	3,001	612-8,780
			Max	9	3,458	1,255-5,226
	6013	TRF	Min	1	1,449	
			Max	1	1,571	
	6133 (cv. Llanero)	TSSF	Min	20	2,288	147-6,105
			Max	24	4,265	233-9,193
		TRF	Min	21	3,308	103-9,915
			Max	23	4,502	794-22,520
	6369	TSSF	Min	6	1,891	133-3,527
			Max	10	3,155	1,071-7,245
		TRF	Min	7	2,021	313-5,153
			Max	10	2,339	510-5,400
	6705	TSSF	Min	1	1,632	
			Max	1	3,246	
		TRF	Min	1	1,005	
			Max	1	2,188	
	6707	TSSF	Max	1	1,917	
		TRF	Min	2	954	593-1,316
			Max	2	3,222	2,077-4,366
	6709	TSSF	Min	1	1,748	
			Max	1	4,418	
	16876	TSSF	Max	1	2,289	

(Continued)

Appendix. (Continued.)

Species	CIAT accession no. (cultivar)	Ecosystem[b]	Season[c]	Number of sites	DM yield over 12 weeks (kg/ha)	
					Mean	Range
B. jubata	16530	TSSF	Max	1	1,605	
	16542	TSSF	Max	1	3,301	
B. nigropedata	6386	TSSF	Min	1	1,110	
			Max	1	1,325	
B. ruziziensis	6019	TSSF	Min	2	1,256	317-2,195
			Max	2	6,229	2,271-10,188
		TRF	Min	4	2,501	1,293-4,143
			Max	3	2,955	997-6,635
	6291	TSSF	Min	1	867	
			Max	1	2,022	
	6419	TRF	Min	1	0	
			Max	1	496	
	16102	TSSF	Min	1	1,425	
			Max	1	2,649	
B. subquadripara	16740	TSSF	Min	1	1,131	
			Max	1	1,778	

a. RIEPT = Red Internacional de Evaluación de Pastos Tropicales (International Tropical Pastures Evaluation Network).

b. TSSF = tropical semievergreen seasonal forest; TRF = tropical rain forest.

c. Min = period of minimum rainfall; Max = period of maximum rainfall.

d. 9-week yields.

e. Distributed as *B. brizantha*, but reclassified as *B. decumbens* by S. A. Renvoize (1993, unpublished report).

SOURCE: RIEPT database.

Chapter 15

Regional Experience with *Brachiaria*: Tropical America--Savannas

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Abstract

The savanna ecosystem is varied and extensive, covering about 250 million hectares in South America. It is characterized by a well-defined dry season and acid, low-fertility soils. A few *Brachiaria* species have shown wide adaptation and are extensively used as pasture grasses in this ecosystem. These were introduced from Africa in the 1950s and 1960s, and spread, at first, vegetatively and then by seed, covering today an estimated 70 million hectares.

Despite constraints—susceptibility to spittlebugs—and nutritional limitations, the few available cultivars, derived from these early introductions, play a major role in livestock production systems in the savannas.

New germplasm has become available since the late 1980s, when collecting trips were undertaken in East Africa, and intensive evaluation programs were developed throughout the region. Selected accessions are entering advanced stages of evaluation.

The results summarized in this paper attest to the outstanding characteristics of some of the new accessions, particularly of *B. brizantha*, and emphasize the importance of collaborative multidisciplinary work between research institutions and countries.

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Introduction

Livestock production in tropical America relies largely on pastures, either native or planted to introduced species. In regions with intensified production and pasture renovation, cultivated pastures have become increasingly important in improving cattle performance. African savanna grasses may be suitable because these evolved under intensive grazing by large ruminants, whereas native South American grasses suffered less herbivore pressure (Parsons, 1972). The spread of African grasses to the American tropics was a massive ecological invasion of some species during colonial times (Parsons, 1972). However, intentional introduction and evaluation of *Brachiaria* accessions did not occur until 30 years ago, with a later intensified effort after germplasm, collected in Africa and brought to CIAT, was made available in 1987.

This paper reviews evaluations of *Brachiaria* accessions and cultivars in the savanna ecosystems of four countries: Brazil, Colombia, Venezuela, and Paraguay. The different savanna ecosystems where *Brachiaria* is being used are characterized, followed by a brief historical background on the introduction of *Brachiaria* for each country. Results of experimentation in individual countries are then presented.

Savanna Ecosystems in South America

Savanna ecosystems in South America are diverse and widespread (Figure 1). The most relevant subecosystems are the cerrados and the llanos.

Figure 1. Distribution of savannas in South America (from Cochrane et al., 1985; P. G. Jones, M. Rincón, and L. A. Clavijo, 1992, unpublished report).

The cerrados are isothermic, well-drained savannas (Cochrane et al., 1985), covering about 203 million hectares or about 22% of Brazil's territory (Adámoli et al., 1985). The vegetation has been described by Eiten (1972). Average annual precipitation ranges from 500 to 2,500 mm, with a well-defined dry season that lasts from 5 to 7 months in 80% of the cerrados. Annual average temperature ranges from 18 to 26 °C. Solar radiation is high, averaging a daily 364 cal/cm^2. Oxisols (especially dark-red and yellow Latosols) are predominant over 56% of the area (Cochrane et al., 1985). These are generally deep, well-drained soils, with low water-retention capacity, high aluminum saturation and phosphorous fixation, and low pH and availability of such nutrients as Ca, S, and Zn.

The savannas are subject to extreme biotic stress: fungal and bacterial diseases are endemic, and leafcutting ants and other insects attack both crops and pastures (Spain and Ayarza, 1992).

The llanos, classified as isohyperthermic savannas, cover about 17 million hectares in Colombia (i.e., about 15% of the national territory) and 30 million in Venezuela (i.e., about 30%) (Silva and Moreno, 1993; Vera and Seré R., 1985). They are characterized by a total wet-season potential evapotranspiration of 900-1,060 mm, a wet-season of 6-8 months and a wet-season mean monthly temperature higher than 23.5 °C. Only a narrow strip in the western part, the Andean foothills (or piedmont) belongs to the tropical semievergreen seasonal forest or the tropical rain forest ecosystems (Cochrane et al., 1985).

Mean annual precipitation in the Colombian Llanos ranges from about 1,600 mm in the eastern Llanos to 5,000 mm in the western piedmont region, and occurs, depending on the location, from February or late April to the second half of November or December (FAO, 1965). Soils are predominantly Oxisols characterized by poor chemical properties: low base status, low pH, high Al saturation, and deficiencies of N, P, K, S, Ca, Mg, and some trace elements (Cochrane et al., 1985).

Rainfall in the Venezuelan Llanos ranges from 700 to 2,000 mm/year, with a 3 to 6-month dry season; mean minimum and maximum temperatures are 21 and 29 °C, respectively. Soils are of medium to low fertility but, in contrast with soils of the Colombian Llanos, they generally do not show high levels of aluminum saturation (Ewel et al., 1976; MAC, 1960).

Although most of the region consists of well-drained savannas, a significant area—the Casanare Plains north of the Meta River, Colombia, and half of the Venezuelan Llanos—is characteristically flooded seasonally (Cochrane et al., 1985; Ministerio de Agricultura y Cría, Anuarios Estadísticos 1950-1978, cited in Chacón, 1991).

Vegetation surveys have been carried out in parts of this region, and the prevailing pasture-based livestock systems described (FAO, 1966; Plessow, 1985; Ramia, 1967; Tamayo, 1964; Vera and Seré R., 1985).

History and Importance of *Brachiaria* Species in the Savannas

Parsons (1972) described the early introduction of African grasses to the American continent. The six species introduced in massive quantities during early colonial times (*Panicum maximum, Brachiaria mutica, Melinis minutiflora, Hyparrhenia rufa, Pennisetum clandestinum*, and *Digitaria decumbens*) were very aggressive and readily disseminated, either by seed or tillers, colonizing better soils in the new continent.

Brazil

The African *Brachiaria mutica* and *B. plantaginea* and, probably, the American *B. extensa* (now *B. platyphylla*)

were first introduced into Brazil during colonial times, according to Sendulsky (1978).

The first introduction of *B. decumbens* was made in 1952 by the Instituto de Pesquisa Agropecuária do Norte (IPEAN), Belém, Pará, under the name of *B. brizantha* (Serrão and Simão Neto, 1971). In 1965, the same material was reintroduced from Suriname, this time as *B. decumbens*. True *B. brizantha* was also introduced to Belém in 1965. *Brachiaria decumbens* was subsequently distributed to other states in Brazil, mainly by tillers because seed production was poor. This accession, referred to as "IPEAN" (BRA-000191/CIAT 6012), has no commercial importance nowadays.

A second ecotype of *B. decumbens* was introduced to the State of São Paulo by the Instituto de Pesquisas IRI (IRI) in the early 1960s, from Australia (Sendulsky, 1978). This material (BRA-001058/CIAT 606) was registered as cv. Basilisk in Australia in 1973 (Mackay, 1982; Stür et al., Ch. 17, this volume). Large quantities of seed were imported from Australia (Hopkinson et al., Ch. 8, this volume; Santos Filho, Ch. 9, this volume), and these, together with governmental programs, helped stimulate the "Cerrado colonization" in Brazil.

The first reports on agronomic performance of these and other *Brachiaria* accessions (*B. brizantha*, *B. ruziziensis*, and *B. arrecta*, syn. *B. radicans*) were published in several states (Costa and Rodrigues, 1971; Monteiro et al., 1974; Tenório et al., 1970). Toxicity (a form of anemia) was soon reported in cattle grazing *B. arrecta* pastures (Souto, 1978; Lascano and Euclides, Ch. 7, this volume), together with a blight caused by the chinch bug, *Blissus* (Hemiptera). These two constraints provoked a ban on the import and commercialization of this species (Leitão Filho, 1977; Valério et al., Ch. 6, this volume).

By 1975, *B. decumbens* cv. Basilisk had become a monocrop over large areas of the savannas and problems such as spittlebug attacks and photosensitization in cattle grazing these pastures stimulated the search for other species. Ecotypes of *B. humidicola* (UF 717 and IRI 409 = CIAT 6013) performed well in trials (Buller et al., 1972; Simão Neto and Serrão, 1974) and interest for this species grew throughout the Amazon (Galvão and Lima, 1977).

An ecotype of *B. brizantha*, introduced in 1967 from Zimbabwe to IRI in São Paulo (IRI 822), was later evaluated by EMBRAPA. In 1984, it became the first officially released cultivar of *Brachiaria* in Brazil: cv. Marandu, registered as BRA-000591 (CIAT 6294; syn. CIAT 6297 and 6780) (Nunes et al., 1984; Keller-Grein et al., Ch. 2, this volume). It proved resistant to spittlebugs but, because it requires better soils, its use in the savannas is restricted.

Colombia

The first introduction of an African *Brachiaria* species into Colombia dates back to the mid-19th century, when *B. mutica*, which may originally have reached the New World as bedding material in slave ships, was carried from Venezuela to the Santa Marta area. From there, it spread rapidly to other parts of Colombia (Parsons, 1972).

An accession of *B. brizantha* was introduced in 1955 from Trinidad and first established at the Palmira research station of the Instituto Colombiano Agropecuario (ICA) in the Cauca valley (Cuesta M. and Pérez B., 1987). By 1966, it was reported as among the most promising species evaluated at two of ICA's research stations: Palmira and "La Libertad" near Villavicencio, in the southwestern Llanos. This accession was released in Colombia as cv. La Libertad in 1987 (Cuesta M. and Pérez B., 1987).

In the mid-1960s, *B. decumbens* cv. Basilisk was introduced to the "La Libertad" station and, in 1972, to the ICA-CIAT research station at Carimagua, in the Colombian Llanos. It was soon

Table 1. Estimated area of pastures in the Puerto López-Puerto Gaitán region of the Colombian Llanos.

Type of pasture	Area (ha)[a]			
	1989		1992	
Brachiaria spp.[b]	76,409	(82.7)	130,640	(75.6)
Other grasses	8,051	(9.1)	11,142	(6.4)
Total pure grass pastures	81,460	(91.8)	141,782	(82.0)
Pure legume sward[c]	323	(0.4)	277	(0.2)
Brachiaria spp. + *S. capitata*	2,337	(2.6)	27,460	(15.9)
Other associations	4,613	(5.2)	3,320	(1.9)
Total area of improved pastures	88,733	(100.0)	172,839	(100.0)
Total area of native savanna	871,459		853,145	
Total area of pastures	960,336		1,025,984	

a. Percentage of total area of improved pastures shown in parentheses.

b. In descending order: *B. decumbens*, *B. humidicola*, *B. dictyoneura* cv. Llanero.

c. In descending order: *Stylosanthes capitata*, *Arachis pintoi*, *Centrosema acutifolium*, *Pueraria phaseoloides*.

SOURCES: Adapted from J. V. Cadavid and R. Botero, 1992, unpublished report; J. V. Cadavid, C. Seré R., R. Botero, and L. Rivas, 1990, unpublished report.

included in the ICA regional trials conducted at several ranches, where it showed excellent environmental adaptation. It has become the most common forage grass in sown pastures in the Llanos (Jiménez C., 1979; J. V. Cadavid and R. Botero, 1992, unpublished report; J. V. Cadavid, C. Seré R., R. Botero, and L. Rivas, 1990, unpublished report).

An accession of *B. humidicola* was introduced in 1976 to the Colombian Llanos from Fiji via the United States Department of Agriculture (USDA) and the Ecuadorean Instituto Nacional de Investigaciones Agropecuarias (INIAP). The accession attained importance as a forage grass in the region because of its vigorous, dense, sward-forming growth habit, and tolerance of low-fertility, poorly drained soils and heavy grazing (CIAT, 1986). This accession (CIAT 679) was released in Colombia as cv. Humidícola (Pérez B. and Lascano, 1992).

Brachiaria dictyoneura (CPI 59610 = CIAT 6133)[1], a more recent introduction from Zambia, reached CIAT in 1978 through the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia. The accession was first established in nursery plots at Carimagua in 1979 (CIAT, 1986). Numerous trials were conducted, leading to its release in Colombia as cv. Llanero (ICA, 1987). Since 1992, it has increasingly been used in the Llanos as pasture grass because of its good performance in low-fertility soils, high seed production, tolerance of spittlebugs, and ease of association with legumes.

By 1992, *Brachiaria*-based pastures, with or without legumes, were mainly of *B. decumbens* and *B. humidicola*, and occupied about 92% of the total area of improved pastures in the Puerto López-Puerto Gaitán region of the Colombian Llanos (J. V. Cadavid and R. Botero, 1992, unpublished report; J. V. Cadavid, C. Seré R., R. Botero, and L. Rivas, 1990, unpublished report) (Table 1). In the entire country, about 3 million hectares are sown to *Brachiaria* species, particularly *B. decumbens* (R. A. Pérez B., 1995, personal communication).

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

Venezuela

Research with a formally introduced *Brachiaria* species in Venezuela dates back to 1949 when *B. decumbens* came, in the form of vegetative material from Trinidad, to Aragua state (Zerpa and Villalobos, 1952). At that time, a widely used grass was *B. mutica* (earlier known as *Panicum purpurascens*), a species naturalized in seasonally flooded environments. Systematic evaluation of *Brachiaria* species, however, began only in the 1970s and dealt with *B. mutica, B. arrecta* (syn. *B. radicans*), *B. decumbens, B. ruziziensis*, *B. brizantha*, and *B. humidicola*. The most recent *Brachiaria* introduction was *B. dictyoneura* CIAT 6133 in 1985 (Flores et al., 1992).

Literature on research with *Brachiaria* in Venezuela is scarce. Introductory evaluations of a range of forage species, including accessions of *Brachiaria*, concentrate on nonsavanna regions such as the humid tropics south of the Maracaibo Lake (MAC, 1975) and the Orinoco Delta (Lárez et al., 1975). More recent reports refer to work conducted in savanna ecosystems such as the seasonally flooded Mantecal site in Apure state (Torres, 1983) and well-drained sites in the states of Guárico (Arias et al., 1985; Mata, 1989), Anzoátegui (Sanabria and González, 1983), and Monagas (FONAIAP, 1985). A comprehensive overview of productivity and quality of forage species introduced to the Venezuelan savannas, including some *Brachiaria* species, is presented by Arriojas and Chacón (1989) and will be discussed later.

Paraguay

In Paraguay, the expansion in the use of the genus *Brachiaria* follows the same pattern as in Brazil. It started in the early 1960s and increased significantly in the 1980s, as more seed became available. Today, even more area is planted, because of easy access to the Brazilian seed market, and the substitution of *P. maximum* pastures by *Brachiaria* species, which demand less fertilizer. The estimated area planted to *Brachiaria* pastures in Paraguay is about 2 million hectares (R. Heyn, 1995, personal communication).

Germplasm Evaluation in the Brazilian Cerrados

Grasses of the *Brachiaria* genus are extremely important forages for cattle production in Brazil. Spain and Ayarza (1992) describe an impressive land use change in South American savannas in the past 25 years. Over 40 million hectares are planted to pastures and 12 million to annual crops, resulting in rapid expansion of both grain and cattle production. Carrying capacity was increased from 0.4 head/ha on native savanna pasture in 1950, to 0.7 head/ha in 1980, a 73% increase due mainly to the use of improved pastures, especially *Brachiaria* (FIBGE, 1990, cited by Ghisi, 1991).

The choice of cultivars for improved pastures has been extremely limited but the few commercial cultivars of *Brachiaria* have shown good adaptation and production. These reproduce by apomixis (i.e., asexually through seed; Valle and Savidan, Ch. 10, this volume), resulting in extensive areas planted to a single genotype. Consequently, problems such as the massive attack of spittlebugs (Homoptera:Cercopidae) have arisen (Valério et al., Ch. 6, this volume).

Despite important constraints, *Brachiaria* cultivars make an impressive contribution to animal production in Brazil and will certainly continue to do so, especially with the release of new cultivars.

Development of new cultivars depends on germplasm diversity, which was virtually nonexistent in America until a large collecting effort was undertaken by CIAT and the International Livestock Centre for Africa (ILCA, now ILRI), under

the auspices of the International Board for Plant Genetic Resources (IBPGR, now IPGRI) and collaboration of national institutions in six East African countries (Keller-Grein et al., Ch. 2, this volume).

In 1987, EMBRAPA introduced a large *Brachiaria* germplasm collection from CIAT, and agronomic evaluation began in both the Cerrados Agricultural Research Center (CPAC, its Portuguese acronym) and the CNPGC.

Planaltina, Distrito Federal. More than 340 accessions of 12 *Brachiaria* species were evaluated in small plots at CPAC (Planaltina, DF), beginning in 1987 (CIAT, 1989a; 1990b; 1991a; Grof et al., 1989). Of the collection, 52% comprises accessions of *B. brizantha*, by far the most variable and promising species represented. Dry matter (DM) yields for the best adapted accessions, 85% of which were *B. brizantha*, ranged from 16 to 21 t/ha over four harvests in the rainy season. Dry-season DM yields were considerably lower, although several accessions performed better than the commercial checks.

Twenty-four accessions were selected from the previous study and compared with cv. Marandu in a small-plot experiment (Grof, 1989). Several accessions of *B. brizantha* outyielded cv. Marandu when cut at intervals of 3, 6, 9, or 12 weeks. Four accessions, representing distinct growth forms with specific agronomic characteristics, were selected for evaluation under grazing: CIAT 26110, 16315, 16306, and 16488.[2]

A severe infestation by spittlebugs occurred at CPAC in late 1988, allowing host-plant reaction to be assessed. Some materials exhibiting the lowest nymph populations also produced very little forage, many being *B. jubata* accessions. However, five accessions of *B. brizantha*, or 3.5% of the 141 accessions evaluated showed very low infestation and good production (B. Grof, unpublished data).

The 24 *Brachiaria* accessions selected at CPAC, were tested for spittlebug resistance under field conditions in an experiment conducted in Goiás state, between 1987 and 1990 (Sobrinho et al., 1992). Nineteen *B. brizantha* accessions and five *B. decumbens* accessions were planted in an old paddock of *B. ruziziensis*, infested with spittlebugs. Three accessions performed better than cv. Marandu, the resistant control: CIAT 16311, 16315, and 16319.

Another trial at CPAC compared root distribution of two accessions (CIAT 16467 and 16488) with those of cvs. Marandu and Basilisk on two types of soil (Carvalho et al., 1992). For both soils, 60% of the root systems were in the top 30 cm. The cultivars had better root distribution in the more fertile soil with a higher water table, whereas the accessions did better on the poorer soil with a lower water table. Overall, the two accessions produced higher dry weight of roots than the cultivars in both soils, displaying good adaptation and soil colonization. Root growth may be another attribute to be included in the selection of new cultivars for adaptation to stressful soil conditions.

Campo Grande, Mato Grosso do Sul. Evaluation of *Brachiaria* germplasm at CNPGC (Campo Grande, MS), began in 1988, with the objective of selecting superior *Brachiaria* accessions for release to ranchers (Valle and Miles, 1994; Valle et al., 1992; 1993a).

Of 320 accessions planted in small plots and subjected to periodic cutting, 11 superior accessions of *B. brizantha*, one of *B. jubata*, and two of *B. humidicola* were selected (Table 2) and multiplied to enter regional agronomic and grazing trials.

Brachiaria brizantha presented the widest diversity and the highest production. The selected accessions have

2. The respective BRA- numbers are BRA-004308; BRA-003441; BRA-003361; and BRA-004391.

Table 2. Agronomic performance of *Brachiaria* accessions evaluated from 1988 to 1991, in Campo Grande, MS, Brazil.

Species (no.)[a]	TDM[b]	TFDM[c]	% TDM-DS[d]	RGV[e]	TGDM[f]
B. brizantha					
Mean collection (96)	9.7	4.8	19	2.6	6.5
Check cv. Marandu	12.0	6.5	17	3.0	8.5
Mean selected (11)	12.6	6.9	17	3.1	9.2
B. decumbens					
Mean collection (35)	5.5	2.4	16	2.1	3.8
Check cv. Basilisk	11.7	5.1	23	2.5	8.4
B. humidicola					
Mean collection (21)	6.2	3.2	13	2.7	4.5
Check (commercial)	6.7	3.0	17	2.3	4.8
Mean selected (2)	9.0	4.8	10	3.0	6.5
B. jubata					
Mean collection (11)	4.1	1.3	16	2.3	2.8
Selected accession	4.6	2.3	16	3.0	3.3

a. Number of accessions in parentheses.
b. TDM = total dry matter production, t/ha.
c. TFDM = total foliar DM production, t/ha.
d. % TDM-DS = percentage of TDM accumulated during the dry season.
e. RGV = vigor of regrowth 7 days after cutting, visual score.
f. TGDM = total green dry matter (leaves + culms) production, t/ha.

SOURCE: Valle and Miles, 1994.

a high leaf-to-stem ratio, fast regrowth after cutting, and good seasonal distribution of total production. These materials are being rated for spittlebug resistance (Valério et al., Ch. 6, this volume). No *B. decumbens* accession performed better than cv. Basilisk, particularly for resistance to spittlebugs. Two *B. humidicola* accessions ranked better than the commercial check.

Other studies were carried out on this germplasm collection at CNPGC, such as detailed morphological characterization (Almeida et al., 1989; Valle et al., 1993b; Keller-Grein et al., Ch. 2, this volume), mode of reproduction in all accessions that flowered (Valle, 1990; Valle and Glienke, 1991), and chromosome counts for most of the sexual material of the collection and some apomictic accessions (Miles and Valle, Ch. 11, this volume).

Digestibility of nine accessions was evaluated at CNPGC, using in situ methods (Nicodemo et al., 1991). The large differences in initial digestibility and rates of disappearance among these selected accessions justify further studies on the quality of *Brachiaria* accessions (Lascano and Euclides, Ch. 7, this volume).

A new group of about 200 accessions was introduced from CIAT in 1994 and will undergo agronomic evaluation at CNPGC, beginning in October 1995.

These results obtained from trials in Brazil highlight the large variation in agronomic traits that exists within species. The prospects for successfully selecting new cultivars from this collection are excellent. Nineteen accessions have been selected at CPAC and CNPGC for regional agronomic trials and grazing trials in 1995 (Appendix 1).

Germplasm Evaluation in the Colombian Llanos

Small-plot evaluation

Limited germplasm base. Much of the agronomic evaluation of *Brachiaria* in the Colombian Llanos has been

conducted at the ICA-CIAT research station in Carimagua. Before 1987, two small collections of *Brachiaria* species were evaluated for environmental adaptation. Of the 18 accessions of eight *Brachiaria* species tested during the late 1970s and early 1980s, *B. brizantha* CIAT 664 (introduced from Puerto Rico; reclassified as *B. decumbens* by S. A. Renvoize, 1993, unpublished report) and *B. dictyoneura* CIAT 6133 (now cv. Llanero) were selected for further evaluation in association with legumes (Grof, 1982a). Outstanding attributes of these accessions were rapid spread by stolons (CIAT 664), and high seed production (CIAT 6133), compared with *B. humidicola* CIAT 679 (CIAT, 1982).

In 1983, a set of 19 new accessions of *B. brizantha, B. decumbens, B. humidicola, B. nigropedata*, and *B. ruziziensis* were included in a small-plot cutting trial. *Brachiaria brizantha* accessions CIAT 6674 and 6385 followed by CIAT 6681, 6675, 6387, and 6384 were the highest yielding accessions and showed high field resistance to spittlebug (CIAT, 1986).

Comprehensive germplasm base. CIAT scientists have begun screening a large collection of *Brachiaria* germplasm, assembled during the CIAT-ILCA collecting mission in Africa in 1984/85 (Keller-Grein et al., Ch. 2, this volume). The list of materials evaluated between 1987 and 1994 includes 376 accessions of 12 *Brachiaria* species, of which *B. brizantha* comprised 52% and *B. decumbens, B. humidicola*, and *B. ruziziensis* together, another 35%.

The first part of this collection, comprising 265 accessions of *B. brizantha, B. decumbens*, (true) *B. dictyoneura, B. humidicola, B. jubata, B. ruziziensis*, and several other *Brachiaria* species, was established in 1987 in small plots within an existing *B. decumbens* pasture known to be infested with spittlebugs (CIAT, 1988; 1989b). The field evaluation emphasized the identification of spittlebug-resistant *Brachiaria* accessions. High incidence of spittlebugs caused severe damage in a majority of accessions during 1988, blighting the control accession *B. decumbens* cv. Basilisk (CIAT 606) completely.

Five *B. brizantha* accessions—CIAT 6690, 16126, 16338, 16827, and 16829—and the spittlebug-resistant check, cv. Marandu (CIAT 6297), were selected for a small-plot grazing experiment at Carimagua, using *Centrosema acutifolium* as the associated legume (CIAT, 1989b; 1990a). These accessions and 26 additional selections were tested in a clipping trial conducted at Carimagua and at ICA's "La Libertad" research station (CIAT, 1991c). The objective was to further assess adaptation to acid, low-fertility soils and resistance to spittlebugs—spittlebug pressure was higher at "La Libertad" (CIAT, 1990c). The checks were *B. decumbens* cv. Basilisk and *B. dictyoneura* cv. Llanero.

Considerable infestation by spittlebugs, however, occurred only at Carimagua, but cv. Marandu and *B. brizantha* accessions CIAT 16827, 16829, and 16961 were not infested. *Brachiaria brizantha* cv. La Libertad (CIAT 26646) showed susceptibility to the insect and the susceptible check *B. decumbens* cv. Basilisk had the highest population of spittlebug nymphs (S. L. Lapointe, 1994, personal communication). The accessions CIAT 16827 and 16829 proved to be outstanding and were recommended for further testing (G. Keller-Grein, unpublished data).

Between 1991 and 1994, a second set of 186 accessions from 10 different species of *Brachiaria* were evaluated in small plots at Carimagua. Two fertilization levels were tested: one that is currently recommended for pasture establishment in the area and the second, higher one, for establishing upland rice. Fertilization did not affect DM yield, N or P contents, or in vitro DM digestibility (IVDMD) of leaves. Liming, however, significantly increased the Ca content of leaves in the higher fertilization level

(Rao et al., Ch. 4, this volume; G. Keller-Grein, unpublished data). Considerable inter- and intraspecific variation was registered for various important plant attributes, such as seasonal DM production, leaf-to-stem ratio, N, P, and Ca content of leaves, IVDMD, flowering time, and seed production (G. Keller-Grein, unpublished data).

In another trial, 53 *B. humidicola* accessions were evaluated, along with commercial checks (*B. humidicola* CIAT 679, *B. brizantha* cv. La Libertad, *B. decumbens* cv. Basilisk, and *B. dictyoneura* cv. Llanero), to identify environmentally adapted accessions with better nutritive value (N content and IVDMD; Lascano and Euclides, Ch. 7, this volume) and seed production at low latitudes than the commercial cv. Humidícola (CIAT 679). The variation registered among accessions for these attributes and DM production is presented in Table 3.

Table 3. Performance of a germplasm collection of *Brachiaria humidicola* (55 accessions) at Carimagua in the Colombian Llanos.

Characteristic	Mean	Range
DM yield, rainy season (g/m^2)[a]	61	25-116
DM yield, dry season (g/m^2)[b]	19	8-37
N content, rainy season (% in leaf DM)[c]	1.03	0.85-1.21
IVDMD, rainy season (% in leaf DM)[d]	65.4[d]	60.2-69.5
Flowering onset (no. of days after standardization cut)[e]	62	45-131
Seed production (g/m^2)[f]	1.97	0.07-7.81

a. Values over six harvests with 6 weeks of regrowth each.
b. Values over two harvests with 6 weeks of regrowth each.
c. Values over five analyses.
d. Values over three analyses.
e. Standardized on 8 April 1994.
f. Continuously hand-harvested during the 1994 rainy season.

SOURCE: G. Keller-Grein, R. Schultze-Kraft, and R. Herrmann, unpublished data.

As a result of these germplasm evaluation trials, the following accessions have been selected for further testing: *B. brizantha* CIAT 16212, 16327, 16776, 26032, 26124, 26318, 26554, 26556, and 26562; *B. decumbens* CIAT 26180; and *B. humidicola* CIAT 16867, 16871, 16886, 26159, and 26427 (G. Keller-Grein, unpublished data).

Regional evaluation. Within the International Tropical Pastures Evaluation Network (RIEPT, its Spanish acronym), 14 agronomic trials (type Regional Trial B according to the methodology applied by RIEPT; Toledo, 1982) have been conducted since the early 1980s in the Colombian Llanos at different sites. These trials have included *B. dictyoneura* cv. Llanero and a few accessions each of *B. brizantha*, *B. decumbens*, *B. humidicola*, and *B. ruziziensis*. Performance of the germplasm in terms of seasonal dry-matter production during 12-week growth periods is summarized in Appendix 2 at the end of the chapter. Accessions that showed good adaptation across locations were *B. brizantha* CIAT 6780 (cv. Marandu), *B. dictyoneura* CIAT 6133 (cv. Llanero), and *B. humidicola* CIAT 679 (cv. Humidícola).

Evaluation under grazing. A series of small-plot grazing trials, including various *Brachiaria* species and accessions, has been conducted at the Carimagua research station, to study the compatibility of adapted grasses and legumes and their persistence in mixtures. Large-scale grazing experiments to measure animal performance are discussed by Lascano and Euclides (Ch. 7, this volume).

***Brachiaria-Desmodium* associations.** An acceptable percentage of legume was maintained in a grazing trial of two *B. brizantha* accessions (CIAT 664 and 665, recently reclassified as *B. decumbens*), each associated with *Desmodium canum* (now *D. incanum*). In an association with *B. dictyoneura* CIAT 6133, however, the same legume was the weaker competitor in the sward (CIAT, 1983).

Satisfactory legume contents were recorded in a 2-year rotational grazing trial for *D. incanum* CIAT 13032 in association with *B. brizantha* CIAT 664 and 6370, and *B. humidicola* CIAT 6369 (Grof, 1985b).

Brachiaria decumbens cv. Basilisk and *A. gayanus* CIAT 621 (now cv. Carimagua 1) were each evaluated in association with *D. ovalifolium* CIAT 350 (now cv. Itabela) (Grof, 1982b). *Brachiaria decumbens* formed a more stable association with this aggressive legume than did *A. gayanus*, which was dominated by the legume. In another trial (Grof, 1984), total (grass + legume) annual DM yields were highest for the association of *D. ovalifolium* CIAT 350 with *B. humidicola* CIAT 679, followed by the association with *B. decumbens* cv. Basilisk, and lowest for the association containing *A. gayanus*. Growth rates and annual yields of the legume did not differ significantly in association with *B. decumbens* cv. Basilisk and *B. humidicola*.

Cultivar Humidícola was the highest and cv. Llanero the lowest yielding grass of five accessions of *Brachiaria* (*B. brizantha* CIAT 664, 665, and 6298, *B. dictyoneura* cv. Llanero, and *B. humidicola* cv. Humidícola) that were evaluated between 1982 and 1985 in association with eight accessions of *D. ovalifolium*. These results were related to selective grazing of cv. Llanero, which is the more palatable grass, but the less tolerant of spittlebug attack (CIAT, 1986).

***Brachiaria-Arachis pintoi* associations.** Comparing different species and accessions of *Brachiaria*, the highest growth rate and total annual DM yield of *A. pintoi* CIAT 17434 (cv. Maní Forrajero Perenne) were recorded in association with cv. Llanero (Grof, 1985a). Legume content in associations with *B. brizantha* CIAT 664, *B. dictyoneura* cv. Llanero, *B. humidicola* cv. Humidícola, and *B. ruziziensis* CIAT 6291 increased with time, to as much as 36% and 44% in cv. Llanero and cv. Humidícola pastures, respectively. The highest legume contents occurred in the associations with *B. brizantha* (72%) and *B. ruziziensis* (almost 70%) because spittlebug attack permitted the legume to colonize the areas left by the grass.

In a subsequent trial (CIAT, 1989b), with other *B. humidicola* accessions (CIAT 679, 6369, 6705, and 6709) and *B. brizantha* cv. Marandu, the proportion of *A. pintoi* increased over time, leading to legume dominance in the associations with CIAT 6369 and 6709 at the end of the experiment. The other associations were more balanced. Grazing pressure had no effect on the performance of these associations.

***Brachiaria-Centrosema acutifolium* associations.** Five selected accessions of *B. brizantha* (CIAT 6690, 16126, 16338, 16827, and 16829) and *B. brizantha* cv. Marandu as check were tested in association with *C. acutifolium* as common legume. During 2 years of grazing (Oct. 1991 to Oct. 1993) CIAT 16827 and 16829 were the most productive and persistent, performing similarly to cv. Marandu, whereas grass productivity and content markedly decreased in the other associations, leading to suspension of grazing after the first year (E. A. Cárdenas, 1994, personal communication).

Germplasm Evaluation in the Venezuelan Llanos

It is noteworthy that most of the recent data on *Brachiaria* evaluation in Venezuela were generated in trials conducted within RIEPT. Despite the scarcity of documented research on the evaluation and cultivar development of *Brachiaria* species, several species have become important pasture plants for the Venezuelan savannas.

The area sown to *Brachiaria* species was recently estimated as being between 2.4 and 4 million hectares, two-thirds of which are planted to *B. decumbens* (A. J. Flores and E. Chacón,

1994, personal communication). This is about 50% of the estimated total area of improved pastures in Venezuela, including savanna and nonsavanna regions.

Brachiaria mutica and *B. arrecta* (syn. *B. radicans*) are valuable grasses for pasture improvement in poorly drained environments. In 1983, 500,000 and 165,000 ha, respectively, were planted to these grasses (MAC-OTE, cited in Chacón, 1991). In intensive production systems, average daily liveweight gains of 750-880 g/animal have been achieved (Matos and Betancourt, 1991).

Brachiaria decumbens, *B. humidicola*, and *B. brizantha* are key species for pasture development in well-drained savannas, but they have also spread to nonsavanna regions (A. J. Flores, 1994, personal communication). The genetic material that is used in Venezuela represents mainly the Australian cvs. Basilisk (*B. decumbens*) and Tully (*B. humidicola*), and the Brazilian cv. Marandu (*B. brizantha*), known in the country as cvs. Barrera (or Alambre), Aguja, and Gigante, respectively (Keller-Grein et al., Ch. 2, this volume). In 1983, about 200,000 ha were planted to *B. decumbens* (MAC-OTE, cited in Chacón, 1991), whereas no estimates have been made of the area planted to the other, more recently introduced, cultivars.

Brachiaria dictyoneura CIAT 6133 was released by the Fondo Nacional de Investigaciones Agropecuarias (FONAIAP) in 1992 as cv. Pasto Ganadero (Flores et al., 1992). It is regarded as superior to *B. decumbens*, *B. humidicola*, and *B. brizantha* in its ability to recover after heavy grazing, drought, or fire. Rate of adoption, however, is constrained by limited availability of seed (A. J. Flores, 1994, personal communication).

Insufficient seed availability is a constraint to greater adoption of *Brachiaria* cultivars. Seed production is limited to small areas in some states, with commercial yields ranging from 15 to 80 kg/ha. *Brachiaria humidicola* is considered as a poor seed producer and *B. dictyoneura* CIAT 6133 as good (A. J. Flores, 1994, personal communication).

Damage by spittlebugs (species of *Aeneolamia* and *Zulia*) constitutes the major biotic constraint to *Brachiaria* production in Venezuela. It is more severe in the western region (including high-rainfall, nonsavanna areas) than in the east. Recently, damage by a *Scaptocoris* species (Hemiptera:Cydnidae) has been observed in Monagas State on *B. brizantha*, *B. decumbens*, and *B. humidicola* (Vásquez et al., 1992). Rust caused by *Uromyces setaria-italicae* has been reported for *B. humidicola* in the States of Lara and Zulia; *Macrophomina* sp. for *B. brizantha* in the States of Anzoátegui, Bolívar, and Monagas; and *Phoma* sp. for *B. dictyoneura* CIAT 6133 in Anzoátegui. The incidence of the latter two diseases seems to be associated with severe drought stress (A. J. Flores, 1994, personal communication).

The only published information available on the practical aspects of establishment, management, and persistence of *Brachiaria* pastures in the Venezuelan savannas is the summary by Arias M. et al. (1984). The Universidad Central de Venezuela (UCV), Maracay, conducted research on the use of phosphorus fertilizer (mainly rock phosphate) on pastures, including *B. decumbens*, *B. humidicola*, and *B. brizantha* (Arriojas et al., 1991; Rodríguez, 1993; E. Chacón, 1994, personal communication).

Preliminary observations suggest that, on farm, even under heavy grazing, particularly persistent associations on sandy soils are *B. dictyoneura*/*Stylosanthes capitata* and *B. dictyoneura*/*Centrosema brasilianum*. In contrast, *C. macrocarpum* and *C. pubescens* have not persisted in association with *B. dictyoneura* CIAT 6133 (A. J. Flores, 1994, personal communication).

A. J. Flores (1994, personal communication) also suggests that, in

eastern Venezuela, N-P-K fertilization at 50 kg/ha is general practice for pasture establishment. Subsequent maintenance comprises applications of 50 to 150 kg of urea/ha per year. Where such maintenance fertilization is not applied, pastures degrade severely (*B. brizantha* the worst, followed by *B. decumbens* and *B. humidicola*). On a yearly basis, *Brachiaria* pastures are stocked with as many as 2 cattle/ha, and grazing management ranges from 3 to 4-week rotational systems to continuous grazing, and even includes occasional hay-making. Overgrazing is common.

The demand for improved pastures in Venezuela is so high that the *Brachiaria* technology developed in neighboring Brazil and Colombia is adopted—and eventually adjusted by farmers to local needs—without major formal testing.

Another important research priority is to ascertain the potential role of *Brachiaria* pastures in integrated crop/livestock production systems (similar to those of Colombian Eastern Plains; CIAT, 1991b) in the Venezuelan savannas.

Brachiaria Evaluation in Paraguay

Brachiaria pastures cover about 2 million hectares in Paraguay. *Brachiaria decumbens* occupies about 200,000 ha, *B. brizantha* 150,000, and *B. humidicola* 21,000 ha in the Chaco region. Nearly 350,000 ha are planted to *Brachiaria* in the west of the country, on light-textured, acid soils (R. Heyn, 1995, personal communication).

Annual DM yields of commercial cultivars range from 7 t/ha for common *B. humidicola* to over 11 t/ha for *B. brizantha* cv. Marandu and 14 t/ha for *B. decumbens* (Heyn and Valinotti, 1989). The same authors recorded annual DM yields of 10 t/ha for *B. brizantha* in association with *C. pubescens* or *Galactia striata*.

Fifteen accessions selected at CPAC, Brazil, were recently evaluated at Itapua, Paraguay (Heyn, 1992). Annual DM yields reported were much higher than those of existing cultivars, ranging from 24 to 50 t/ha for the first year and 19 to 32 t/ha in the second year of evaluation, although some accessions (e.g., *B. brizantha* CIAT 16128) maintained or even improved production in the second year. These preliminary results demonstrate the potential for several *B. brizantha* accessions in the subtropical rain forest ecosystem, where low temperatures occur (annual mean temperature of 21.5 °C, with one to two frosts per year).

Concluding Remarks

Brachiaria pastures are of unquestionable importance in the savanna ecosystem. Despite insufficient technical information, the widespread adoption and use of *Brachiaria* species speak for the broad adaptation and resilience of the few cultivars available, even under less than optimal conditions.

In recent years, new germplasm became available and extensive agronomic evaluation was undertaken. Limitations in existing cultivars have been defined, and techniques for screening large germplasm collections have been developed. Promising new accessions are in advanced stages of evaluation and will soon become available.

Obviously, evaluation techniques need to be perfected, and regional trials need to be carried out in savanna environments different to those reported here. That would help define the range of adaptation, patterns of use, and certainly, the potential role of different accessions in integrated crop/livestock production systems.

Pests and diseases constrain *Brachiaria* pastures only in a relatively narrow section of the savanna ecosystems. However, these constraints need to be

considered in a selection program because the wide adoption of a new cultivar, particularly if it is established in monoculture, could bring about heavy biotic pressures.

Brachiaria is and will continue to be the foremost genus for the acid and low-fertility soils of the tropical savannas. The genus, therefore, merits that considerable resources be dedicated to the selection of new and improved cultivars.

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References

To save space, the following acronyms are used in place of publishers' names:

ASAP-Qld. = Australian Society of Animal Production, Queensland Branch

CPAC = Centro de Pesquisa Agropecuária dos Cerrados

ETES = Estudio Técnico y Económico de Sistemas de Producción Pecuaria

FONAIAP = Fondo Nacional de Investigaciones Agropecuarias

ICA = Instituto Colombiano Agropecuario

INRA = Institut national de la recherche agronomique

MAC = Ministerio de Agricultura y Cría

NZGA = New Zealand Grassland Association

NZIAS = New Zealand Institute of Agricultural Science

NZSAP = New Zealand Society of Animal Production

SBZ = Sociedade Brasileira de Zootecnia

TGSA = Tropical Grasslands Society of Australia

UCV = Universidad Central de Venezuela

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Appendix 1. Accessions Selected at CPAC and CNPGC for Good Agronomic Performance on Well-drained Savannas (Brazilian Regional Trials, 1995).

Species	Accession number	
	BRA-	CIAT
B. brizantha	002801	16121
	002844	16125[a]
	003000	16150
	003204	16288
	003247	16294
	003361	16306
	003387	16308
	003395	16309[a]
	003441	16315
	003450	16316[a]
	003484	16319
	003719	16441[a]
	003824	16457
	003891	16467[a]
	003948	16473[a]
	004308	16488[a]
	004391	26110[a]
B. humidicola	005011	16886
	005118	26149
Checks		
cv. Basilisk	001068	606
cv. Marandu	000591	6297
commercial *B. humidicola*	-	679

a. Advanced to grazing trials at CNPGC, Campo Grande, MS, Brazil.

SOURCE: C. B. do Valle, 1994, unpublished data.

Appendix 2. Seasonal Dry-matter Production of *Brachiaria* Species in the Colombian Llanos, During RIEPT[a] Type B Trials.

Species	CIAT accession no. (cultivar)	Site	Dry-matter production[b] over 12 weeks (kg/ha)	
			Wet season	Dry season
B. brizantha	664[c]	Alto Menegua	902	708
		Bonanza	1,519	1,409
		Guadalupe	616	266
		Pachaquiaro	970	1,809
	6653[c]	Carimagua	2,403	5,553[d]
	6294 (cv. Marandu)	Alto Menegua	1,315	1,625
		Bonanza	1,551	1,358
		Guadalupe	1,195	150
		Pachaquiaro	955	1,280
	6387	Las Leonas	4,160	889
	6780 (cv. Marandu)	Iracá	2,103	266
		La Alegría	3,233	480
		La Reserva	2,751	503
		Las Leonas	4,081	963
		Morichito	1,997	930
	26646 (cv. La Libertad)	Iracá	1,669	674
		Morichito	1,760	1,221
B. decumbens	606 (cv. Basilisk)	Carimagua	3,187	508[d]
		El Paraíso	1,523	340
		El Viento	1,258	536
		Guayabal	493[e]	116
		Iracá	1,744	485
		Morichito	1,736	1,427
		Orocué	1,897	240
	6131	Orocué	-	450
	6699	Alto Menegua	1,435	1,507
		Bonanza	1,476	1,358
		Guadalupe	1,323	176
	6700	Alto Menegua	892	689
		Bonanza	1,268	1,039
		Guadalupe	1,190	240
		Pachaquiaro	842	1,403
B. dictyoneura	6133 (cv. Llanero)	Alto Menegua	1,588	1,111
		Bonanza	2,201	802
		Carimagua, La Alegría	4,081	584
		Carimagua, La Reserva	3,352	433
		Orocué	2,725	430
		Guadalupe	733	370
		Iracá	1,190	910
		Morichito	1,942	892
		Pachaquiaro	1,139	2,282
B. humidicola	679 (cv. Humidícola)	Carimagua	2,422	242[d]
		El Paraíso	2,669	785
		Las Leonas	5,391	973
		Orocué	4,340	293
	6369	Alto Menegua	1,209	240
		Bonanza	1,242	806
		Guadalupe	586	60
		Iracá	1,680	942
		Morichito	1,157	616
		Pachaquiaro	1,035	2,031
	6705	Alto Menegua	1,106	280
		Bonanza	2,158	1,277
		Guadalupe	1,690	203
		Pachaquiaro	1,460	2,593

(Continued)

Appendix 2. (Continued.)

Species	CIAT accession no. (cultivar)	Site	Dry-matter production[b] over 12 weeks (kg/ha)	
			Wet season	Dry season
B. humidicola	6707	Alto Menegua	1,676	200
		Bonanza	2,393	1,033
		Guadalupe	998	160
		Pachaquiaro	1,176	1,537
B. ruziziensis	6419	Alto Menegua	1,011	280
		Bonanza	973	776
		Guadalupe	682	20
		Pachaquiaro	819	1,000

a. RIEPT = Red Internacional de Evaluación de Pastos Tropicales (International Tropical Pastures Evaluation Network).

b. First year of evaluation.

c. Recently reclassified as *B. decumbens* (S. A. Renvoize, 1993, unpublished report).

d. 8-week regrowth.

e. 9-week regrowth.

SOURCES: Pizarro, 1982; 1985; 1992.

Chapter 16

Regional Experience with *Brachiaria*: Sub-Saharan Africa

J. Ndikumana* and P. N. de Leeuw**

Abstract

In tropical Africa, the most common and most extensively evaluated *Brachiaria* species as cultivated pastures are *B. brizantha*, *B. ruziziensis*, *B. decumbens*, and *B. mutica*. In recent years, *B. dictyoneura* cv. Llanero, *B. humidicola*, and *B. platynota* have also received increased attention. The first four species produce high yields, show excellent response to fertilizer, are persistent, and remain green long into the dry season. Although, in Africa, data on nutritive value are incomplete and scattered, they indicate that forage from *Brachiaria* is highly palatable to stock, leading to high intake, whether fed fresh or grazed in situ. These species have also shown broad adaptation to different ecological zones. Although some may be drought-resistant, they perform best in the subhumid and humid zones where rainfall exceeds 800 mm and the growing season is more than 6 months. Low temperature depresses growth; therefore, *Brachiaria* in general, performs poorly at altitudes above 1,800 m. Further research is needed to place selected ecotypes of *Brachiaria* and other perennial forage species in the context of farming systems and develop integrated crop-livestock production systems for sub-Saharan Africa.

Introduction

The center of diversity of the genus *Brachiaria* is in eastern and central Africa (Renvoize et al., Ch. 1, this volume), from where some species have been introduced into tropical regions of the Americas (Argel and Keller-Grein, Ch. 14, this volume; Pizarro et al., Ch. 15, this volume), Southeast Asia, and northern Australia (Stür et al., Ch. 17, this volume), often revolutionizing grassland farming and animal production. According to Boonman (1993), *Brachiaria* species are common and valuable constituents of the natural vegetation in East Africa. Sown pastures play essentially no role in livestock production in Africa, except in smallholder dairies in the highlands, and even here it is cut-and-carry forage, rather than extensive grazed pasture, that is important. Evaluation of *Brachiaria* for pasture improvement began in the 1950s in Kenya, Nigeria, Uganda, Tanzania, and Zaire, the most common and extensively evaluated species being *B. brizantha*, *B. ruziziensis*, *B. decumbens*, and *B. mutica*. In recent years, *B. dictyoneura*[1], *B. humidicola*, and *B. platynota* have received increased attention.

This review focuses on assessing (1) dry matter (DM) yield of germplasm accessions; (2) agronomic attributes (such as establishment and drought tolerance) and responses to management inputs (such as fertilizer application and cutting intervals); (3) compatibility and performance in associations with herbaceous and tree legumes and as leys in rotation with crops; (4) interactions between yield and

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1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero

nutritive value in response to management; and (5) performance of ruminants on pastures or on forage for stall feeding.

Germplasm Evaluation

Results from agronomic small-plot trials are summarized in Table 1, according to the major ecological zone where the trial was carried out. They show the wide range of adaptation of the species tested.

The RABAOC Project

Multilocational forage evaluations have been conducted by the project Réseau de recherche en alimentation du bétail en Afrique Occidentale et Centrale (RABAOC). The project is a collaborative research network organized by the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), CIAT, and the International Livestock Centre for Africa (ILCA, now ILRI). It covers nine countries of western and central Africa, at 10 sites representing a wide range of environmental conditions (RABAOC/AFRNET, 1995).

The evaluations involved assessing an initial establishment phase of 12 weeks, followed by 2 years of observations. Dry matter accumulation over 12 weeks, following a standardization cut, was measured twice each year, once during the rainy and once during the dry season, according to the method described by R. Schultze-Kraft and J. M. Toledo (1990, unpublished report).

Results aggregated from eight sites show that the four *Brachiaria* species evaluated grew well in the region (Table 2) and gave high yields throughout the year. *Brachiaria brizantha* CIAT 26646 was the best overall performer across sites in the first year, followed by *B. decumbens* CIAT 606; *B. dictyoneura* CIAT 6133 gave the best yields in the second year.

Agronomic Attributes

Establishment

Brachiaria is readily established by seed or vegetative material—either stem cuttings or "splits" (divisions, with roots, of an established plant).

Establishment rates from splits averaged 76% and from cuttings, 60%, in 1955 at Yangambi, Congo Belge (now Zaire), according to the Institut national pour l'étude agronomique du Congo Belge (INEAC). Experiments conducted by Capelle in 1974 demonstrated that removal of the upper and lower glumes from the spikelets induced quick and vigorous germination of *B. ruziziensis* seeds (INEAC, 1955, cited in Ndikumana, 1985).

At Rubona, Rwanda, *B. ruziziensis* achieved 77% soil cover 2 months after planting, and 87% cover 5 months after planting on a low-fertility soil. In its 1955 experiments, INEAC found that, after dry-season harvests, this species showed faster regrowth than any other grass species tested in the study (INEAC, 1955, cited in Ndikumana, 1985).

Brachiaria brizantha and *B. decumbens* were quickly established from seeds, splits, or cuttings. At Kijansoa, Madagascar, *B. brizantha* established rapidly from cuttings, so that a first harvest could be taken after 45 days (Granier and Lahore, 1966). However, in Madagascar and Burundi, *B. brizantha* and *B. decumbens* developed more slowly than *B. ruziziensis*, reaching maximum yield only in the second or third year after planting; *B. ruziziensis* showed higher growth rate and yield during the first year than in subsequent years (ISABU, 1993).

Flowering and seeding

At Kitale in Kenya, located near the equator, *B. ruziziensis* flowered 21 weeks after sowing, while regrowth headed as early as 3 weeks after cutting (Boonman, 1971). INEAC's 1958 studies in Congo Belge (now Zaire) showed that, on

Table 1. Dry matter (DM) production of unfertilized *Brachiaria* species in the humid and subhumid zones of sub-Saharan Africa.

Site	Country	Altitude (m.a.s.l.)	Annual rainfall (mm)	Species	DM yield (t/ha)	Growth period	Reference
Humid zone							
Pokoase	Ghana	152	1100-1200	*B. ruziziensis*	3.7	5 months	P. Barnes, 1994, unpublished report
Kijansoa	Madagascar		1650	*B. ruziziensis*	12	1st year	Granier and Lahore, 1966
				B. brizantha	12	1st year	Granier and Lahore, 1966
Not known	Mauritius			*B. ruziziensis*	17.2, 21.5	1974, 1978	Jotee, 1988
				B. brizantha	15, 18.7	1974, 1978	Jotee, 1988
Subhumid zone							
Nyankpala	Ghana	305	1080	*B. ruziziensis*	4.3	5 months	P. Barnes, 1994, unpublished report
Shika, Zaria	Nigeria	600	900-1100	*B. decumbens*	10-16	Annual yield	Agishi, 1979, unpublished data
Moso	Burundi	1300	1000	*B. brizantha* CIAT 664	15.3	Annual yield	ISABU, 1988, unpublished report
				B. ruziziensis	8.3	Annual yield	ISABU, 1988, unpublished report
				B. brizantha, 5 accessions	4.4-9.3	Annual yield	ISABU, 1993
				B. decumbens, 6 accessions	2.4-6.2	Annual yield	ISABU, 1993
				B. jubata, 1 accession	0.8	Annual yield	ISABU, 1993
Lowland sites		800	850	*B. brizantha*, local	14	2nd year peak	ISABU, 1992, unpublished report
				B. decumbens, local	18.5	2nd year peak	ISABU, 1992, unpublished report
				B. ruziziensis, local	2.5	1st year peak	ISABU, 1992, unpublished report
Medium altitude sites		1300-1500	1000	*B. ruziziensis*, local	12.1	1st year peak	ISABU, 1992, unpublished report
				B. brizantha, local	4.2	3rd year peak	ISABU, 1992, unpublished report
				B. decumbens, local	7.1	3rd year peak	ISABU, 1992, unpublished report
Morogoro	Tanzania	500	860	*B. brizantha*	3.6	Annual yield, 10-year-old	Frederiksen and Kategile, 1980
Tanga		66	1506	*B. ruziziensis*	9.2	Annual yield	Hopkinson, 1970
Not known	Mauritius			*B. ruziziensis*	17.5, 30.6	1976, 1978	Jotee, 1988
				B. brizantha	21.4, 29.2	1976, 1978	Jotee, 1988
Highlands							
7 sites	Burundi	1900-2200		*B. brizantha*	8.5	2nd year peak	ISABU, 1992, unpublished report
				B. decumbens	8.5	2nd year peak	ISABU, 1992, unpublished report
				B. ruziziensis	5.0	1st year peak	ISABU, 1992, unpublished report
Uyole	Tanzania	1800	870	*B. ruziziensis*	1	3-year mean	Urio et al., 1988

Table 2. Performance of *Brachiaria* accessions across eight sites in western and central Africa.

Species	CIAT accession no.	Soil cover at 12 weeks (%)	DM yield over 12 weeks (t/ha)		Dry-to-wet season ratio
			Dry season	Wet season	
B. brizantha	6780	63	4.1	8.6	0.48
B. brizantha	26646	56	3.2	5.6	0.32
B. decumbens	606	69	3.8	8.6	0.45
B. dictyoneura	6133	68	3.0	6.8	0.44
B. humidicola	6369	65	1.6	4.1	0.38
LSD (P <.05)		16	1.1	2.2	

SOURCE: Adapted from RABAOC/AFRNET, 1995.

low-fertility soils, plants flowered after 2 months, while on more fertile soils they flowered after 4 months, with or without fertilizer (Ndikumana, 1985). Blouard and Behaeghe (1961) reported differences in seed set between sites in the forest or savanna zones, demonstrating that seed set is influenced by climatic conditions; they also reported differences among accessions.

Under favorable conditions, *B. ruziziensis* yields up to 140 kg/ha of seed. In Kenya, seed yield increased with fertilizer level, with the maximum yield in the second year after establishment (Boonman, 1971).

Drought tolerance

Trials in the Belgian Congo (now Zaire) at Gimbi and Mvuazi by INEAC in 1958 showed that *B. ruziziensis* was among the most persistent forages in heavily grazed pastures during the dry season (Ndikumana, 1985). In 1965, in experiments conducted by the Institut de recherches agronomiques tropicales (IRAT, now CIRAD-CA), *B. ruziziensis* showed satisfactory productivity over a 5 to 6-month dry season, provided annual rainfall reached 800-900 mm. This was confirmed by experiments in Senegal (Birie-Habas, 1965) and Côte d'Ivoire (Boudet, 1962), which showed that *B. ruziziensis* did not persist where the dry season exceeded 7 months.

At Sangalkam, Senegal (<500 mm rainfall), Boyer (1986) found that *B. brizantha*, with cumulative yields of 6 t/ha DM, was more drought tolerant than *Andropogon gayanus*, which yielded 5 t/ha.

In Madagascar and at several other sites, *B. brizantha* and *B. decumbens* remain green during the dry season, when most other forage grasses become yellow and highly lignified. At Kijansoa, root mass of *B. brizantha* was 180 g/plant, compared with that of *B. ruziziensis*, which was only 18 g/plant. Roots of *B. brizantha* penetrated deeper in the soil, explaining its higher tolerance of drought (Granier and Lahore, 1966).

Persistence

Data from Burundi, Madagascar, Nigeria, and Tanzania suggest that few grass species are more aggressive and persistent than *B. brizantha*. At the Institut des sciences agronomiques du Burundi (ISABU), *B. brizantha* and *B. decumbens* gave consistently higher yields than *B. ruziziensis* up to 3 years after planting. In Madagascar, *B. brizantha* rapidly invaded adjacent grazing areas and persisted even under frequent grazing and severe trampling (Granier and Lahore, 1966), and in Tanzania, swards of this species persisted for 20 years, despite frequent harvesting (Urio et al., 1988).

Response to Management

The major findings of those experiments that focused on productivity and nutritive value under different spacings,

fertilization, and cutting regimes, mostly in the humid and subhumid zones, are reviewed here.

Okeagu and Agishi (1990) examined the effect of planting density (20 x 20, 40 x 20, or 60 x 20 cm) and N level (basal dressing superphosphate at 22 kg P/ha plus 0, 100, or 200 kg/ha N) on *B. decumbens* at Shika, Zaria, Nigeria. Increasing planting density from 8 to 25 rooted splits/m^2 increased yield by 75% in the first and 30% in the second year, but gave no advantage in the third year. Maximum DM yields were 6.3 t/ha, at 12.5 splits/m^2, without fertilizer. Response to fertilizer N was small, with maximum yield of 7.3 t/ha DM at 200 kg/ha N the first year. Yield increases per kg of N applied averaged 3.5 kg DM in the first year and 11 kg in subsequent years. In the second and third year, maximum yield was 8.1 t/ha at 200 kg/ha N, after 4.5 months of growth. Nitrogen application increased crude protein (CP) content from 6.1% to 9.4%, maximum content coinciding with maximum DM yield. The highest CP yield (700 kg/ha) was obtained with 200 kg/ha N (versus 280 kg/ha CP in the control)—an N recovery rate of 33%.

In 1980, a study was conducted at Sangalkam, Senegal, to determine seasonal variation in response to fertilization of irrigated *B. mutica* (Mandret et al., 1990). Growth curves of DM production were established for the cool dry season (November-March), the warm dry season (March-July), and for the rainy season (July-October). With 150 kg/ha N, DM yields of 6 months' regrowth were 3.7 t/ha during the cool dry season, 5.9 t/ha during the warm dry season, and 11.3 t/ha during the rainy season. Although low temperatures depressed overall productivity of *B. mutica*, N fertilization reduced this effect, improving productivity in the cool dry season.

The effects of three cutting intervals (20, 40, or 60 days) and four rates of N application (0, 100, 200, or 400 kg N/ha) on the yield and CP content of *B. brizantha* were studied over 120 days at Morogoro, Tanzania. Cumulative DM yield increased with increasing N rates and less frequent cutting (E. J. Mtengeti and A. B. Lwoga, 1989, unpublished report) (Table 3). The leaf-to-stem ratio was not affected ($P > .05$) by N rate but decreased ($P < .01$) with longer cutting intervals. Crude protein content of the herbage declined with longer cutting intervals, but increased from 6.9% to 12.9% when N was increased from 0 to 400 kg/ha. Crude protein yield increased with increasing cutting interval up to the 40-day interval. It was concluded, therefore, that at Morogoro, Tanzania, *B. brizantha* should be harvested at about 6-week intervals to strike a balance between herbage yield and quality.

Table 3. Effect of fertilizer rate and cutting interval on cumulative dry matter (DM) yield and N efficiency of *Brachiaria brizantha* at Morogoro, Tanzania.

Fertilizer rate (kg/ha)	Cutting interval (days)[a]					
	20		40		60	
	Yield (t/ha)	Efficiency[b]	Yield (t/ha)	Efficiency[b]	Yield (t/ha)	Efficiency[b]
0	1.3a	-	2.1a	-	1.3a	-
100	3.0a	16.5	3.5a	13.9	3.5a	18.8
200	5.4b	20.2	5.5b	17.1	5.6b	22.6
400	5.1b	9.3	7.6c	13.7	7.6b	18.0

a. In each column, means followed by the same letter are not significantly different ($P < .05$).

b. Yield increase over control in kg DM/kg N applied.

SOURCE: E. J. Mtengeti and A. B. Lwoga, 1989, unpublished report.

Another trial, conducted at Makerere University Farm, Kabanyolo, Uganda, demonstrated that the highest yield response of *B. mutica* (55 kg DM/kg of N applied) was obtained with the lowest rate of fertilizer N applied (224 kg N/ha). Very high rates of fertilizer (1,792 kg N/ha) resulted in the lowest yield response and did not increase DM yields as much as CP contents (14.1% in DM) and therefore, total CP yields per hectare (5.1 t/ha) (Olsen, 1974).

Table 4. Yield of *Brachiaria ruziziensis* and *Panicum maximum* grown in alleys of *Leucaena leucocephala* and *Gliricidia sepium* at Angokame, Benin.

Treatment	Grass yield (t/ha)	
	P. maximum	*B. ruziziensis*
G. sepium	6.8	3.0
L. leucocephala	7.4	3.1
Control without trees	8.0	3.2
Control + fertilizer	8.8	3.4
LSD 5%	0.9	0.5

SOURCE: M. Ehouinsou, 1993, unpublished report.

Productivity of *Brachiaria* Species in Grass-Legume Mixtures

The performance of important *Brachiaria* species in associations with forage legumes has been studied in several sub-Saharan African countries. The most important results are summarized here.

Alley cropping

The effect of alley cropping grass and legume forages on quantity and quality of fodder was studied at Angokame, Benin, in the subhumid zone (ferralitic soil). *Brachiaria ruziziensis* and *Panicum maximum* were planted between hedges of *Leucaena leucocephala* and *Gliricidia sepium* (M. Ehouinsou, 1993, unpublished report). The legume hedges, except on *P. maximum* with *G. sepium* hedges, had no effect on grass productivity (Table 4). However, *L. leucocephala* produced three times as much woody biomass when alley-cropped with *B. ruziziensis* than with *P. maximum*, suggesting more competition for light, water, and nutrients by the latter. The foliar biomass produced by the tree species was not influenced by grass species.

At Minkoa Meyos, a humid site near Yaoundé, Cameroon, the DM yields of *B. ruziziensis* planted between hedgerows of *L. leucocephala* and *G. sepium* were similar and not significantly different from the yield of the control plots without trees (Institut de recherches zootechniques [IRZ], 1981, unpublished report).

Grass-legume associations

At Dschang, Cameroon, *B. ruziziensis* was associated with three forage legumes. The cumulative grass DM yield was higher from grass-legume associations than from pure stands, and higher with *Desmodium uncinatum* than with *D. intortum* or *Stylosanthes guianensis* (Table 5). Total CP yields from

Table 5. Dry matter (DM) and crude protein (CP) yields of *Brachiaria ruziziensis* intercropped with forage legumes at Dschang, Cameroon.

Treatment	Grass yield (t/ha)	Legume yield (t/ha)	Total DM (t/ha)	Proportion of grass (%)	CP yield (t/ha)	CP content of grass (%)
B. ruziziensis alone	1.8 ± 0.2	-	1.8 ± 0.2	100	0.1 ± 0.02	6.3 ± 0.4
B. ruziziensis + *Desmodium intortum*	6.9 ± 0.2	3.3 ± 0.1	10.2 ± 2.0	68	0.8 ± 0.2	5.4 ± 0.4
B. ruziziensis + *D. uncinatum*	8.4 ± 0.9	2.8 ± 0.3	11.2 ± 1.2	75	1.2 ± 0.2	7.1 ± 1.0
B. ruziziensis + *Stylosanthes guianensis*	5.4 ± 0.8	3.4 ± 0.3	8.8 ± 1.0	61	0.7 ± 0.1	5.6 ± 0.2

SOURCE: Njwe et al., 1992.

grass-legume associations were also higher than those from pure stands, the *Brachiaria-D. uncinatum* mixture yielding the highest (Njwe et al., 1992). Crude protein content of *B. ruziziensis* was affected by the associated legume species.

In Minkoa Meyos, Cameroon, J. Kouonmenioc (1993, unpublished report) evaluated the productivity of *B. dictyoneura* CIAT 6133 (cv. Llanero) intercropped with *Centrosema pubescens*, planted simultaneously. The grass became dominant in all plots, even where three grass rows alternated with three legume rows. This shows the high competitive ability of *B. dictyoneura* cv. Llanero in the humid zone.

In the subhumid zone of Nigeria, *B. decumbens* was recommended as a highly promising species for pure grass swards. Akinola (1981) assessed its performance in association with eight forage legumes: *D. uncinatum*, *D. scorpiurus*, *D. tortuosum*, *C. pubescens*, *Macroptilium atropurpureum* (cv. Siratro), *Neonotonia wightii* (cv. Cooper), *S. guianensis* (cv. Schofield), and *S. humilis* (cv. Gordon). The mixture with *D. uncinatum* gave the lowest total yield per year (6.5 t/ha), with a 6% legume content; that with *C. pubescens*, the highest yield (10.2 t/ha) with a 31% legume content. *Centrosema pubescens*, *D. scorpiurus*, *S. humilis*, and *M. atropurpureum* were recommended as compatible companion legumes in swards of *B. decumbens*. Their annual contribution to DM and N yields was sustained and tended to increase with time.

The N and P content of grass and legumes declined with less frequent cutting. When grass was cut at 6-week intervals, N content averaged 1.33% and P content 0.20%; when cut at 8-week intervals, N content was 1.05% and P content 0.19%. The N content of grass in association with *D. tortuosum*, *C. pubescens*, and *D. scorpiurus* exceeded that of grass in pure swards by 10%, 19%, or 30%, respectively.

Grass-cereal rotations

The effect of 3 years of forage leys on subsequent maize yields was evaluated by C. Bodji Nguessan (1994, unpublished report) in central Côte d'Ivoire. The effect of the forage grass species was compared with that of forage legumes and of applied fertilizer. Different *Brachiaria* accessions did not affect subsequent maize yield; *Brachiaria* leys were as effective as applied fertilizer in increasing maize yield (Table 6). Without added fertilizer, grain yields after fallow were lower ($P < .05$). This suggests that the decomposed biomass from the grass ley improved soil fertility, contributing the equivalent of 110 kg/ha N.

In 1981, on-farm trials were carried out at Bako, Ethiopia (1,650 m.a.s.l.), intercropping maize with various forage grasses, including *B. ruziziensis*. Oversowing of *Brachiaria* did not lower maize yields, suggesting that *B. ruziziensis* can be successfully sown into maize to increase feed resources during the dry season (Institute of Agricultural Research [IAR], Ethiopia, 1981, unpublished report).

Table 6. Maize grain yield after 3 years of *Brachiaria* leys in small plots at Bouaké, Côte d'Ivoire.

Species	CIAT accession no. (cultivar)	Grain yield (kg/ha)
B. brizantha	26646 (cv. La Libertad)	3,842
B. decumbens	6780 (cv. Marandu)	3,422
B. dictyoneura	606 (cv. Basilisk)	2,916
B. humidicola	6133 (cv. Llanero)	3,275
Fertilizer application[a]		
None		2,138
200 kg/ha		3,056
400 kg/ha		3,877
LSD_{05}		1,958

a. N, P, and K fertilizer (10-18-18) was applied during soil preparation; in addition, 75 and 150 kg/ha were applied in split portions after emergence and during flowering of male florets.

SOURCE: Adapted from C. Bodji Nguessan, 1994, unpublished report.

Nutritive Value of *Brachiaria* Species

In sub-Saharan Africa, the nutritive value of *Brachiaria* species has been extensively evaluated through chemical analysis and feeding trials. Some of the activities in Nigeria, Tanzania, and Uganda are highlighted here.

Nigeria

At Zaria, Miller and Blair-Rains (1963) assessed the nutritive value of several fodders, including *B. brizantha*, fed to local sheep and zebu cattle. Sheep fed *B. brizantha* cut at full-bloom stage consumed 0.89 kg/day DM, containing 4% CP and 31.1% crude fiber, with 56.6% digestible organic matter and 0.8% digestible CP. The nutritive value was low, as the forage was harvested at an advanced stage of maturity.

At the same location, Onifade and Agishi (1990) reported daily weight gains of 0.59 kg per head for cattle grazing *B. decumbens* pastures at a stocking rate of 6.8 head/ha during 126 days in the rainy season.

At Mokwa, in the southern Guinea savanna of Nigeria, Ruthenberg (1974) showed that adult zebu steers grazing *B. brizantha* pastures at a stocking rate of 625 kg liveweight/ha gained 0.63 kg/day during the rainy season, but hardly any weight in the dry season.

Tanzania

At Morogoro, Frederiksen and Kategile (1980) reported a yield of 800 kg/ha CP in 5 weeks' regrowth of *B. brizantha*. E. N. Nnko (1986, unpublished data) reported that the same plots, when 20 years old and fertilized with 105 kg/ha N, yielded 400 kg/ha of CP after 8 weeks' regrowth. In western Tanzania, Kapinga (1986) reported that, of 11 forages studied, *Brachiaria* species provided the most palatable forage.

At Sokoine University, voluntary DM intake of three forage species was measured, using 16 dairy heifers (Kimambo et al., n.d.). The intake of *B. brizantha*—harvested at postbloom stage and fed fresh *ad libitum*—was higher per cow (7.4 kg/day) than that of *Pennisetum purpureum* (5.2. kg/day) or rice straw (3.9 kg/day). The authors concluded that *B. brizantha* forage for stall feeding could support a moderate level of milk production.

Uganda

Bredon and Hovel (1961), comparing nutritive values of *Brachiaria* species and *Cynodon dactylon*, reported that digestible CP values of *B. brizantha* ranged from 1.2% to 4.8% of DM during the dry season, and concluded that this species could provide above-maintenance feed for cattle during 4-7 months of the year.

At Makerere University, Soneji et al. (1971) used Corriedale sheep to determine voluntary feed intake and in vivo digestibility of three forage species at different stages of growth. Intake and digestibility of *B. ruziziensis* were higher than those of *Chloris gayana* and *Setaria sphacelata* at late growth stages (Table 7). Thus, optimal intake of digestible nutrients probably occurs when pasture utilization of *B. ruziziensis* coincides with the late head stage or early bloom stage of growth.

Table 7. In vivo digestibility (percentage of dry matter) of three grass species at different stages of growth at Makerere University, Uganda.

Species	Phenological stage of growth[a]				
	Boot	Head	Bloom	Seed	Mean
Brachiaria ruziziensis	64.9a	64.2a	60.4b	59.6b	62.3a
Chloris gayana	63.4a	61.0a	54.6b	53.5b	58.1b
Setaria sphacelata	63.0a	60.6a	57.5ab	52.1b	58.3b

a. Means followed by the same letter in a column are not significantly different ($P > .05$).

SOURCE: Soneji et al., 1971.

Conclusions

This review has shown that, in Africa, research has concentrated mainly on a few accessions of four *Brachiaria* species: *B. brizantha*, *B. ruziziensis*, *B. decumbens*, and *B. mutica*. Their high yields, large responses to fertilizer application, persistence, and ability to remain green long into the dry season are some of their positive attributes as forage species. Although, in the African context, data on nutritive value are incomplete and widely scattered, they indicate that forage from *Brachiaria* is highly palatable to stock and conducive to high intakes, whether fed fresh or grazed in situ.

In general, *Brachiaria* species are best adapted to the wetter ecological zones; optimal performance can only be expected in the subhumid and humid zones where rainfall exceeds 800 mm and the growing period lasts at least 5 months. Growth is depressed by low temperatures; so performance is poor at altitudes above 1,800 m.a.s.l.

The modest contribution of African research to current knowledge on *Brachiaria* grasses as forage or pasture plants can be attributed to the traditionally low priority given to pasture science and forage agronomy. Sown pastures play essentially no role in livestock production in Africa, except in smallholder dairies in the highlands, and even here it is cut-and-carry forage, rather than extensive grazed pasture, that is important.

It may appear ironic that commercial use of *Brachiaria* species is so limited on their native African continent, whereas they have become critically important to the extensive cattle production systems based on sown pastures in lowland tropical America (see Argel and Keller-Grein, Ch. 14, this volume; Pizarro et al., Ch. 15, this volume). The limited use in Africa is not based on lack of adaptation to the physical or biotic environment: the results of forage agronomy trials cited in this paper show them to be well adapted, and they are widely recognized as important components of the native African range (Boonman, 1993). Instead, limited commercial use is based on attributes that make them less appropriate than other forages in the livestock production systems prevailing in Africa.

Since the late 1970s, efforts have been directed at adapting station-based research on sown pastures and planted forage to African smallholder farming systems. This shift required that the past emphasis on high-input systems be replaced by research with multiple goals, so that forage species would simultaneously provide livestock feed, improve soil fertility (and thus result in higher yields), and accomplish erosion control. Placing the attributes of *Brachiaria* and other perennial forage species within the context of African farming systems is a task that has only recently been tackled on a continental scale. However, the task has been made easier by the existing broad database on biological productivity of the major species, their management, and their responses to nutrient inputs and harvesting regimes. Thus, a solid foundation exists for developing integrated systems for crop-livestock production for sub-Saharan Africa.

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To save space, the following acronyms are used in place of publishers' names:

AFRNET = African Feed Resources Network

CIRAD = Centre de coopération internationale en recherche agronomique pour le développement

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Chapter 17

Regional Experience with *Brachiaria*: Asia, the South Pacific, and Australia

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Abstract

Brachiaria species occupy about 300,000 hectares in Asia, the South Pacific, and Australia. In Asia and the South Pacific, they are the most widely grown pasture grasses in the humid and subhumid tropics; in Australia, the area to which they are adapted is relatively small, but within it, *Brachiaria* occupies more than half the area of improved pastures. *Brachiaria mutica*, the first species introduced into the region, in the late 1800s, is now widely naturalized. Since seed of *B. decumbens* became available in the early 1970s, this has become the most widely planted species. *Brachiaria humidicola* is popular in wetter areas of Asia and the South Pacific, especially with smallholders. *Brachiaria ruziziensis*, introduced into Australia in the late 1960s, was soon replaced there by *B. decumbens*; however, in recent years, it has been promoted in Northeast Thailand, where a large quantity of seed is produced. The success of *Brachiaria* species can be attributed to their broad adaptation and to their aggressiveness and resilience, which enable them to persist even under unfavorable conditions.

Introduction

Asia, the South Pacific, and tropical Australia present a continuum from largely cropping in Asia, through cropping with some pastoralism in the South Pacific, to pastoralism with some cropping in tropical Australia. Obviously, land use varies within each region and country, but this broad picture reflects the proportion of planted pastures in these systems. In Asia, the planting of forages, either for grazing or stall feeding, is not widespread. Ruminants are generally fed crop residues and naturally occurring vegetation from idle land. This contrasts with tropical Australia, where large areas of planted pastures exist. In the South Pacific, considerable areas of native pasture and some planted pasture are used for cattle production both in the open and under coconuts.

In Asia and the South Pacific, *Brachiaria* species are among the most widely used pasture grasses. *Brachiaria mutica* (paragrass) is naturalized in practically every country in the region, having been introduced into Asia almost 100 years ago. Despite its wide distribution and availability, the total area it occupies is fairly small, because its ecological niche is confined to poorly drained, swampy areas. In such situations, it is widely used by smallholders for buffalo and cattle (Magadan et al., 1974; Snitwong et al., 1983; Vijchulata, 1981). Other *Brachiaria* species have been introduced more recently; however, *B. decumbens* (signalgrass) is well known, and is the grass most widely planted for pasture in the South Pacific (Evans et al., 1993) and in the humid and subhumid tropics of Southeast Asia. *Brachiaria humidicola* (koroniviagrass) is used less than *B. decumbens* in the same countries, but has become more popular in recent years,

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especially among smallholders. *Brachiaria ruziziensis* (ruzigrass) is of local importance in Northeast Thailand and in Kerala State, southwestern India; *B. subquadripara* (korigrass; syn. *B. miliiformis*), in Sri Lanka.

In Australia, *Brachiaria* species are most widely used within a discontinuous subcoastal belt of Queensland, between 16° S and 22° S; they have a minor role further south, in the coastal subtropics. Three species are important commercially: *B. decumbens*, *B. mutica*, and *B. humidicola*. *Brachiaria ruziziensis*, although once important, has passed out of use. The three species used have potential where land is cleared for pasture in the sparsely settled tracts of Cape York Peninsula (Queensland) and Top End (northern part of Northern Territory). They are planted primarily for fattening and breeding beef cattle, but are not popular for dairying. They are also used for seed and hay production, often in rotation with annual crops. To a limited degree, they extend into drier areas under irrigation. *Brachiaria mutica* is used in ponded pasture systems. The belt within which these species thrive represents less than 1% of the Australian land surface, although it includes some of the more productive parts. They are thus of local rather than national importance.

History of Germplasm Introduction

Although many Asian and South Pacific countries had introduced forage species early this century, the systematic evaluation of the germplasm took place mainly in the last 30 years (Chen and Ahmad Tajuddin, 1989; Moog, 1989). Many of the *Brachiaria* species in use reached Asia and the South Pacific via Australia, which was able to supply seed of commercial cultivars. The major source of forage germplasm for researchers in the region has been the Australian Tropical Forages Genetic Resources Center (ATFGRC) of the Commonwealth Scientific and Industrial Research Organisation (CSIRO). In recent years, small quantities of experimental seed have also been supplied by CIAT, Colombia.

Brachiaria mutica was introduced into Australia and the South Pacific in about 1880 (Barnard 1969; Roberts, 1970), and was widely naturalized, even before the great expansion of tropical pastures began in the 1960s. In Asia, *B. mutica* was first recorded in Calcutta in the early 1900s, and was probably introduced from the Dutch East Indies (now Indonesia) (Burkill, 1966). It remains a highly valued grass of swamps; seasonally inundated land, such as the central plain in Thailand (Topark-Ngarm and Gutteridge, 1986); and ponded pastures in Australia. However, because of the limited overall extent of the niches to which *B. mutica* is adapted, the total area planted to it is relatively small.

Brachiaria decumbens was introduced into Australia in 1930 (Barnard, 1969) from the Department of Agriculture, Kampala, Uganda (Oram, 1990), probably by the Council for Scientific and Industrial Research (CSIR, now CSIRO). It was first sown in the subtropics, especially around coastal Brisbane (27° S) (Loch, 1977), where it still grows along the roadsides. In 1936, it was taken to South Johnstone (18° S), in the high-rainfall lowland tropics (Harding, 1972). Here, under much more favorable conditions, it was thoroughly evaluated (Schofield, 1944) and found promising. Its commercial adoption was greatly delayed, however, by a belief that it did not set useful amounts of seed, an error corrected by Grof (1968). Once good quality seed became readily available, its use expanded greatly, and it is now the most popular grass of Queensland's humid tropics. It was approved for commercial release in 1966 and registered in 1973 as the cv. Basilisk (Oram, 1990).

Brachiaria humidicola was introduced as CPI 16707 into Australia in 1952 from Rietondale Experiment Station, Pretoria, South Africa, by J. F.

Miles (Oram, 1990), and initially planted in the subtropics. Samples of the material also went to Fiji and Papua New Guinea in the 1950s. It was taken to South Johnstone in 1965 and later evaluated on a well-drained soil; however, because its cool-season growth was inferior to that of *B. decumbens*, it provided no grounds for release. But meanwhile, expatriate Australians returning in 1973 to the nearby Tully River district from Papua New Guinea brought it with them, and it quickly became popular on wet soils, to which it is better adapted than *B. decumbens*. In retrospective recognition of this, it was formally released as cv. Tully in 1980. It has become much more popular than *B. decumbens* in Top End.

The last commercial species to be introduced into Australia was *B. ruziziensis*, in 1961 (Barnard, 1969; Keller-Grein et al., Ch. 2, this volume). It was evaluated under grazing during 1964-1966 (Mellor et al., 1973) and received some promotion (Davidson, 1966). It was briefly popular, chiefly because its seed was readily available, but was soon virtually eliminated by the far superior *B. decumbens*. Released in 1966, it had effectively disappeared by 1974.

In Australia, because of the success of the available *Brachiaria* species and the absence of any serious pest, such as the spittlebugs of the Americas, there has been little incentive to seek alternative species. Hence, other species, such as *B. brizantha*, are not used. In Asia, seed production of the Australian cultivars is often a problem, and alternative *Brachiaria* species are being evaluated for suitable seed production characteristics.

Environmental Adaptation

The *Brachiaria* species used in the region are adapted to the humid and subhumid tropics. They can be used in dryland pastures with a minimum of about 1,000 mm annual rainfall, but most *Brachiaria* species are used in higher rainfall environments (>2,000 mm), extending into extremely wet situations. Their range of adaptation stretches from areas without dry periods to those with marked seasonal variation in rainfall distribution, some occurring in areas with harsh dry seasons of up to 8 months. Within the general range, each species shows specific preferences, especially in regard to soil drainage characteristics, but also to temperature and water deficit.

Lessons from Australia

In the main production belt, the average mean daily temperature of the warmest month varies with elevation and latitude, but within fairly narrow limits of about 23-26 °C (it is substantially higher, 31 °C, in the relevant districts of the Northern Territory). In the coolest month, mean daily temperature is about 15-22 °C in the tropics, going down to about 13 °C in more marginal coastal areas of the subtropics.

Marked seasonal variation in growth is a feature of all pasture plants in all districts where *Brachiaria* species are used, primarily because of seasonal fluctuations in temperature and rainfall. The relationship between temperature (mean daily temperature being the most useful measure) and growth is only imperfectly understood. The evidence from a few simple experiments (Nada, 1980; Sweeney and Hopkinson, 1975), plus inference from field behavior (Harding and Grof, 1978; Mellor et al., 1973; Whiteman et al., 1985; C. Middleton, 1978, unpublished report), indicate a pattern in which growth rates start to decline as mean temperature falls below about 24 °C, although evidence from behavior of other tropical grasses (Ivory and Whiteman, 1978) suggests that 30 °C may be a more realistic estimate of this point. The decline continues until growth ceases, at about 15 °C in the very sensitive species (*B. ruziziensis* and *B. humidicola*) and about 12 °C in the more tolerant ones (*B. decumbens* and *B. mutica*).

Because falling temperatures coincide with the onset of the dry season,

the dryland species show great seasonal declines in production during this period. To some extent, this decline can be reduced by strategic use of nitrogenous fertilizer during the cool season (Harding and Grof, 1978; Teitzel et al., 1991a).

Brachiaria ruziziensis is adapted to the warmer and wetter end of the climatic range, and only to well-drained soils. The demise of *B. ruziziensis* was related to its sensitivity to drought and low temperatures, which was magnified by its habit of seeding vigorously at the start of the cool dry season (April), at the expense of both new leaf growth and quality of feed (Mellor et al., 1973).

Brachiaria decumbens is much more widely adapted. It tolerates prolonged severe dry seasons, provided some subsoil moisture remains. Its virtue in such conditions is its ability to produce green shoot into the dry season long after other grass species have ceased to grow. It is equally successful in the wettest districts, provided the drainage is good. It persists in the subtropics, even where winters are too cold for it to grow sufficiently to provide useful feed, and has great vigor in the warmest districts.

Brachiaria humidicola will grow on well-drained soils, but does not compete vigorously. It is more sensitive to low temperatures than *B. decumbens* (C. Middleton, 1978, unpublished report), and its useful range, in terms of both latitude and elevation, is narrow. But on wet soils—either because of poor drainage or excessive rainfall—it is unrivalled, and is effectively "the signalgrass of the wet soils."

Brachiaria mutica may grow on dry soils, but never persists under grazing. Its niches are the wettest soils, swamps, and margins of lagoons or man-made ponds. Under these conditions, it has perhaps the greatest range of temperature tolerance and the widest latitudinal distribution.

Experience from Asia and the South Pacific

The Australian experience is supported by observations and experimental data from Asia and the South Pacific. Summarizing experience and research results in the humid tropics of Malaysia, Chee and Wong (1986) recommended *B. decumbens* for well-drained soils, regardless of soil fertility, and *B. mutica* for poorly drained ones. In Thailand, Topark-Ngarm and Gutteridge (1986) recommended *B. mutica* for the seasonally flooded central lowlands; and *B. decumbens* for the cooler highlands in the north and for the drier Northeast, because of its superior dry-season growth.

This attribute of *B. decumbens* was confirmed in an experiment by Thinnakorn and Kreethapon (1993). They evaluated a range of *Brachiaria* species in Northeast Thailand over 4 years, in an area with an average annual rainfall of 1,100 mm and a distinct dry season from November to April (Table 1). Although the variation in annual yield was fairly small, *B. decumbens* provided more feed than other *Brachiaria* species during the dry period, when feed is limited.

An area where *B. ruziziensis* has proved successful as a fodder plant is in the high ranges of central Kerala State in southwestern India (Kerala Livestock Development Board, unpublished data). The district lies at about 10° N, at an elevation of 850-1,000 m. Annual rainfall approaches 3,000 mm, mostly falling in a bimodally peaked, intense, monsoon

Table 1. Dry matter (DM) yield (mean of 4 years) of *Brachiaria* species in Northeast Thailand.

Species	DM yield (t/ha)		
	Wet season	Dry season	Yearly total
B. decumbens	13.8	3.1	16.9
B. mutica	12.4	2.2	14.6
B. miliiformis[a]	12.9	1.1	14.0
B. ruziziensis	12.5	1.4	13.9
B. humidicola	11.4	2.1	13.5

a. Now *B. subquadripara*.

SOURCE: Thinnakorn and Kreethapon, 1993.

season between June and October. May and November are the transitional months, and the remaining 5 months are dry. Average mean daily temperatures range from about 20 °C in the coolest to 26 °C in the warmest month. The area typically has acid, leached podzolic soils that deteriorate under cropping. Grass is grown to be cut for fodder and, to some extent, grazed by tethered cows. Some seed is taken.

Brachiaria ruziziensis in Kerala shows all signs of being well adapted to the conditions, growing vigorously, persisting, and spreading naturally. Its niche in this area is distinct: at higher elevations, too cool for *B. ruziziensis*, it is replaced by *Pennisetum clandestinum* (kikuyugrass); in drier districts near Palghat, where the annual rainfall declines to 2,000 mm and hot winds off the Deccan Plateau create severe dry-season stress, *B. decumbens* is better adapted than *B. ruziziensis*.

Another area where *B. ruziziensis* is widely grown is Northeast Thailand. Soils are sandy and of low fertility, and the annual rainfall averages 1,000 mm. Rain falls mainly between May and October, with a distinct dry season from November to April. Although *B. ruziziensis* is less productive than many other grasses in this environment (Table 1), its high seed yields have made it popular in this area. Seed yields of 600-1,000 kg/ha have been obtained by farmers, and the volume of *B. ruziziensis* seed produced in Thailand increased from 18 t in 1983 to over 600 t in 1992 (Phaikaew and Pholsen, 1993). For seed production, *B. ruziziensis* is often treated as an annual in this environment. Much of the seed produced is distributed to smallholders as part of the "Greening Northeast Thailand" program.

The adaptation of *Brachiaria* species to acid soils is well recognized in Asia. In a germplasm evaluation trial, both *B. dictyoneura* cv. Llanero and *B. humidicola* produced higher yields than other grasses on an acid sulfate soil (pH 3.5) in the humid tropics of Malaysia (Table 2). On less problematic, but nevertheless acid soils, such as those at the Serdang research station of the Malaysian Agricultural Research and Development Institute (MARDI) (well-drained sedimentary soil, pH 4.2), *B. decumbens* and *B. brizantha* were usually among the top-yielding accessions in species evaluation experiments (Wong et al., 1982).

In the South Pacific, *B. decumbens* and *B. humidicola* are the main species used in planted pastures on the wetter islands (>2,000 mm annual average rainfall), with *B. humidicola* being recommended for poorer soils (B. Mullen, 1994, personal communication). In Vanuatu (humid tropics), *B. decumbens* is the most widely sown grass in coconut plantations, and both *B. decumbens* and *B. humidicola* have been recommended for planting, both in the open and under older coconuts (Macfarlane, 1993). On high pH, coralline soils, *B. humidicola* is the preferred species, even in low-rainfall areas (Macfarlane, 1993).

The shade tolerance of *Brachiaria* species ranges from high in *B. subquadripara* (syn. *B. miliiformis*), through medium in *B. decumbens*, *B. brizantha*, and *B. humidicola*, to low in *B. mutica* (Shelton et al., 1987; Wong, 1991).

Table 2. Productivity (mean of 3 years) of fertilized *Brachiaria* species and other forage grasses on an acid sulfate soil (pH 3.5, H_2O) in the humid tropics of Malaysia.

Species	Dry matter yield (t/ha per year)
B. dictyoneura cv. Llanero	17.6
B. humidicola	14.9
B. brizantha	10.6
Panicum maximum	10.0
B. decumbens	9.9
Setaria splendida	8.0
B. mutica	5.7

SOURCE: Aminah and Wong, 1991.

Pests and Diseases

Brachiaria species experience few maladies in Australia, Asia, and the South Pacific. The most severe insect pest of tropical America—spittlebugs (Valério et al., Ch. 6, this volume)—have not been recorded as a problem in the region, and no records exist of outbreaks of pests and diseases on *Brachiaria* in Asia and the South Pacific. In Australia, *B. mutica* suffers occasional to constant plagues of a *Toya* species (a small leafhopper), which can be locally devastating. *Brachiaria decumbens* occasionally goes into a decline associated with high populations of *Pratylenchus brachyurus* and *P. zeae* (root lesion nematodes), especially when fertilized with N, but it always recovers. It is also subject to occasional damage from a range of species of root-feeding beetle larvae (J. M. Hopkinson et al., unpublished data). *Brachiaria humidicola* is frequently infected with a false-smut fungal disease, *Ephelis* sp., which appears to debilitate individual plants but does little overall harm to the sward (QDPI, unpublished data).

Use of *Brachiaria* Species as Pasture Plants

The essential virtue of *Brachiaria* grasses is that they are infinitely forgiving of mismanagement. Their most notable characteristics, in the places to which they are adapted, are their resilience and aggressiveness, which enable them to tolerate overgrazing and to suppress most other competing plants, such as weeds, other pasture grasses, woody regrowth, and, unfortunately, most useful legumes.

An example of the competitiveness of *B. decumbens* is its ability to replace weeds such as *Imperata cylindrica*. Eng and Basery (1991) completely replaced *I. cylindrica* with *B. decumbens* in just over 1 year (Figure 1) by burning

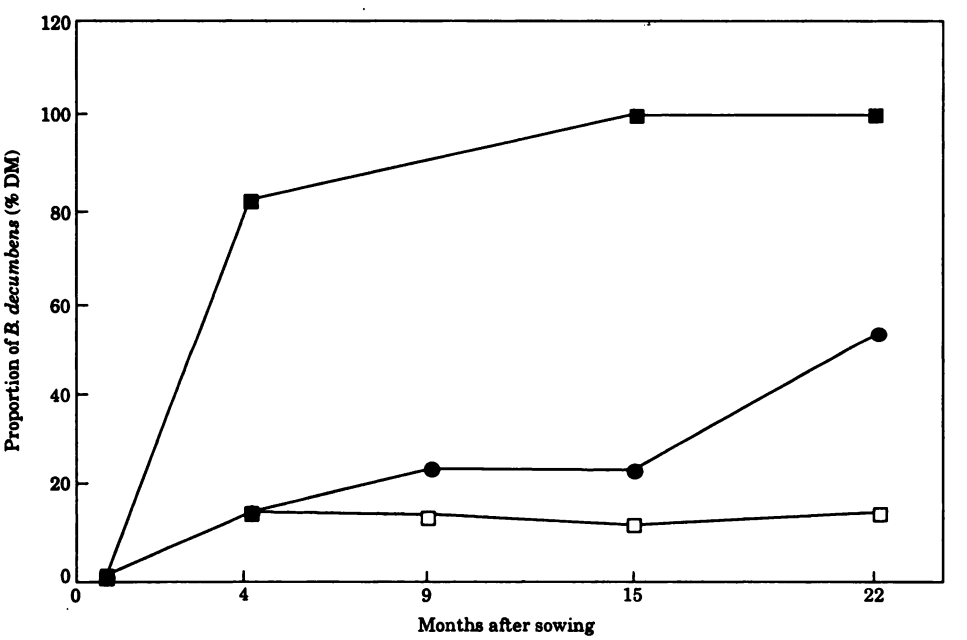

Figure 1. Competitiveness of *Brachiaria decumbens* sown into an *Imperata cylindrica* area in Malaysia (■ = burning + cultivation + 100 kg/ha N; ● = oversowing + 100 kg/ha N; □ = oversowing only; DM = dry matter). (Adapted from Eng and Basery, 1991.)

I. cylindrica, cultivating, sowing *B. decumbens* with a fertilizer application of 100 kg/ha N, and then grazing by cattle. Oversowing, plus 100 kg/ha of applied N increased the proportion of *B. decumbens* to a little over 50% in 2 years. Oversowing without N application had little success.

In Asia and the South Pacific, *B. humidicola* is generally regarded as the most aggressive and resilient of the *Brachiaria* species and is often recommended for smallholders (S. Chand, 1994, personal communication).

The relative incompatibility of *Brachiaria* species with legumes has led to the development of largely monoculture grass pastures. Grazed *B. decumbens* and *B. humidicola* pastures require N fertilizer for high productivity, and, in northern Australia, Teitzel et al. (1974) recommended a yearly use of 200 kg/ha of N. But farmers generally use fertilizer only in prosperous times, and pastures must persist without it for long periods. *Brachiaria decumbens* and *B. humidicola* can tolerate intermittent fertilization better than most other grass species, yet can also respond to higher fertility.

Figure 2 shows an example of the resilience of *B. decumbens*. *Brachiaria decumbens* and *Panicum maximum* (guineagrass) were fertilized with 150 or 300 kg/ha N, and grazed at stocking rates of 6, 8, or 10 hd/ha (Kedah-Kelantan cattle with liveweights of 80-300 kg) in Malaysia (Chen et al., 1981). *Panicum maximum* persisted only when fertilized at 300 kg/ha N and grazed at 6 hd/ha, whereas *B. decumbens* persisted with less N at the same stocking rate. It also persisted at the higher stocking rate of 8 hd/ha when fertilized with 300 kg/ha N.

Nitrogen deficiency reduces the competitiveness of grasses. Thus, in pastures where N is deficient, *B. decumbens* and *B. humidicola* can coexist with locally well-adapted legumes.

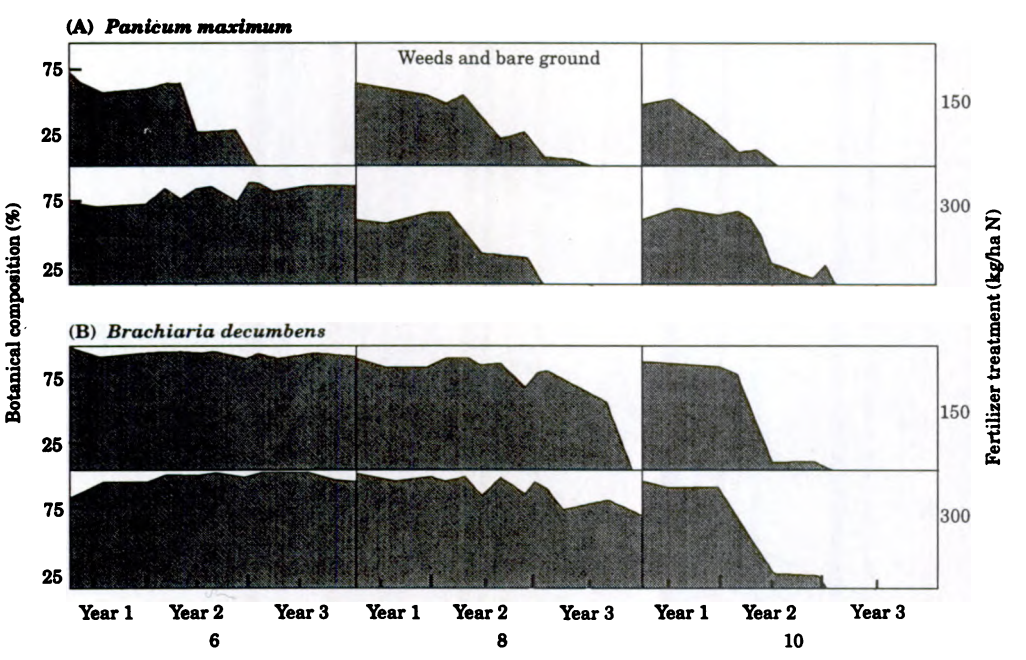

Figure 2. Proportion (%) of (A) *Panicum maximum* and (B) *Brachiaria decumbens* in pastures receiving 150 or 300 kg/ha nitrogen (N) fertilizer and grazed at 6, 8, or 10 head/ha in Malaysia over 3 years. (Adapted from Chen et al., 1981.)

In Australia, *Calopogonium mucunoides* (calopo) combines with *B. decumbens* in the lowland tropics, where the mixed sward can be managed productively with care, despite—or perhaps because of—*C. mucunoides*'s relative unpalatability. *Desmodium heterophyllum* (hetero) has also combined successfully with *B. decumbens* at high-rainfall lowland sites, as has *Vigna parkeri* cv. Shaw at higher elevations. The most promising of available legumes, however, is *Arachis pintoi*, which at a few trial and commercial sites has combined effectively with *B. decumbens* under grazing. *Aeschynomene americana* (jointvetch), particularly the new perennial cv. Lee, offers promise in association with *B. humidicola* in wet areas. Other legumes, such as *Stylosanthes scabra* (seca), show surprising isolated success, especially when the grass is disfavored by low fertility or prolonged overgrazing.

In the South Pacific, the Vanuatu Pasture Improvement Project recommended that smallholders combine *B. decumbens* or *B. humidicola* with *D. heterophyllum*, *Vigna hosei*, *Centrosema pubescens*, *Aes. americana* cv. Glenn, *Ar. pintoi*, and *Ar. repens* (Macfarlane, 1993). In experimental situations in Fiji, *Ar. pintoi* formed stable mixtures with both grasses (S. Chand, cited in Stür and Ndikumana, 1994). Similarly, *B. decumbens* combined successfully with *Ar. glabrata* in a long-term cutting experiment in Indonesia (T. Ibrahim, cited in Stür and Ndikumana, 1994).

Another option is to grow tree legumes with *Brachiaria* pastures. In Malaysia, Izham and Hassan (1984) and Wong et al. (1987) reported good prospects for associations of *B. decumbens* with *Leucaena leucocephala* (leucaena) for beef and dairy production.

Animal Production

On *Brachiaria* pastures, the general picture of animal production, as measured by growth of steers, is that individual growth rates of 0.40-0.50 kg/day liveweight can be maintained, provided ample new green leaf is presented (Table 3). Occasionally, greater gains can be sustained, but only under unusually favorable conditions; for example, high average daily weight gains on *B. mutica* over 3 years came from intensively managed pastures, irrigated, and fertilized with N, in the dry tropics at Parada, Queensland, Australia (J. Evans, 1962, unpublished report).

Usually, animal production is lower under farm conditions. In Asia and the South Pacific, this is often related to low or no fertilizer applications to pastures, although other factors—such as, the accumulation of old plant material after periods of rapid growth, excessive rainfall and cloudiness, trampling damage under wet conditions, and N deficiency—also contribute to poorer production. In the subtropics, reduced sward growth during the cool dry season also results in lower animal production (e.g., Harding and Grof, 1978; Mellor et al., 1973).

Sustainable stocking rates that allow maximum liveweight gain per hectare without sacrificing the pasture vary with season and locality (Table 3), and are primarily a reflection of grass productivity. Rates of 3-5 hd/ha, averaged over the whole year, are used on N-fertilized *B. decumbens* pastures in the wet coastal tropics of Queensland (Harding and Grof, 1978; Teitzel, 1991; Teitzel and Wilson, 1991; Teitzel et al., 1991a; 1991b). These stocking rates fall to about 2-3 hd/ha on the adjacent cooler Atherton Tablelands (700-900 m elevation). Sustainable stocking rates are much lower in situations where soil fertility is low.

In tropical Australia, dairy farmers do not favor *Brachiaria* species, preferring to use other grasses, such as *Setaria sphacelata* and *P. maximum*. This is likely to be related to milk yield, although Wan Hassan et al. (1990) reported no difference in milk yield of Sahiwal x Frisian cows grazing a range of introduced grasses, including *B. decumbens*. Milk yield averaged

Table 3. Cattle production on *Brachiaria* pastures: examples of liveweight gain data from long-term grazing trials in Asia, the South Pacific, and Australia.

Species	Average daily gain (kg/hd)	Stocking rate (hd/ha)	Annual liveweight gain (kg/ha)	Reference[a]
B. decumbens				
Australia, coastal subtropics[b]	0.40	5.0	730	Whiteman et al., 1985
Australia, wet coastal tropics[b]				
(1965-1968)	0.49	4.5	805	Harding and Grof, 1978
(1969-1971)	0.55	5.0	1,004	
(1969-1971)	0.44	7.4	1,188	
Malaysia, wet tropics[b] (1975-1977)	0.35	8.0	902	Chen et al., 1981
Philippines, wet tropics, under coconuts[b] (1991-1992)	0.43	2.0	315	Moog et al., 1993
Solomon Islands, subhumid tropics[c] (1979-1981)	0.43	3.6	557	Smith and Whiteman, 1985
B. humidicola				
Solomon Islands, subhumid tropics[c] (1979-1982)	0.39	3.6	504	Smith and Whiteman, 1985
B. subquadripara (syn. *B. miliiformis*)				
Western Samoa, humid tropics, under coconuts[c] (1976-1978)	0.48	2.3[d]	417	Reynolds, 1981
B. mutica				
Australia, irrigated dry tropics[b]	0.71	3.3	855	J. Evans, 1962, unpublished report
Philippines, humid tropics[b]	0.43	3.0	469	Mendoza, 1984
Solomon Islands, subhumid tropics[c] (1979-1981)	0.50	3.6	662	Smith and Whiteman, 1985
B. ruziziensis				
Australia, wet coastal tropics[b]	0.53	1.25[d]	242	Mellor et al., 1973

a. Where grazing experiments included more than one treatment, only the most productive treatment is quoted.

b. Fertilized with nitrogen.

c. Grass-legume association.

d. Average.

2,000 kg/cow over a lactation period of 350 days. Much higher milk yields were obtained on *B. decumbens* pastures interplanted with leucaena (Wong et al., 1987). In Fiji, *B. mutica* is widely used by dairy farmers (S. Chand, 1994, personal communication).

In experiments in Asia, Abas Mazni and Sharif (1986) reported photosensitization of small ruminants and occasionally of cattle grazing or being fed *B. decumbens* or *B. ruziziensis*. In contrast to the American tropics (Lascano and Euclides, Ch. 7, this volume), photosensitization is seldom a problem in cattle on-farm, particularly if animals have access to other forage species. In Malaysia, sheep graze *B. humidicola* without detrimental effects.

Brachiaria Species in Farming Systems

Brachiaria pastures are not used in isolation, but as components of more complex grazing, feeding, and farming systems that may involve ley pastures in rotation with crops; use of other pasture types; and the feeding of mineral, protein, and energy supplements.

The complementary use of *Brachiaria* with other grass and grass-legume pastures takes many forms, and several such systems have been meticulously detailed by Teitzel et al. (1991b) and Teitzel and Wilson (1991). The particular value of *Brachiaria* paddocks in these systems is that they will serve as sacrifice pastures to carry excess stock numbers in difficult times, thus taking the pressure off other, more vulnerable, pasture types, such as *P. maximum* and *C. pubescens* associations. For example, *B. humidicola* fills this role when conditions are excessively wet, being tolerant of severe trampling. *Brachiaria decumbens* shows particular value in late dry season, being able to produce green pick longer than other grasses in districts with 1,000-1,600 mm annual rainfall and a severe dry season of 5-6 months.

Brachiaria decumbens and *B. humidicola* both play a valuable role in rotational farming in northern Queensland, where they provide a grass break between cropping phases. Their ease of establishment and relative freedom from species of nematodes that affect field crops encourage their use. In mixed farming systems, *B. decumbens* is often sown with maize in the last year of the cropping phase, so that a sward exists by the time the maize is harvested, thus shortening the period of no production and reducing soil erosion risks. The only problem with *B. decumbens* in rotations is the slow breakdown of the dead tussock bases, which are a nuisance in subsequent cultivations.

The grass provides income from seed, hay, or grazing. The best hay of either *B. decumbens* or *B. humidicola* is used to fatten cattle; most of the remaining is fit primarily for weaners and dry cows; and the worst is sold as orchard mulch. Seed-crop hay of *B. decumbens* is prone to mold, owing to the nature of the seed-crop sward, which is usually old, thick, lodged, and has been wet for long periods.

In Australia, conservationists react to pasture development by widely publicizing the fear that many introduced pasture plants may be potential weeds, capable of invading native plant communities. Farmers and agronomists sometimes express a similar fear of the weed potential of introduced pasture species in croplands. Both groups have targeted *B. mutica* and *B. decumbens* as weeds (Lonsdale, 1994).

Brachiaria mutica is indeed a weed of swamps and waterways, particularly where livestock have no access and where water is enriched by nutrients leaching from crop or urban land. It may choke waterways or, by breaking away in floating masses during floods, damage bridges. It invades disturbed native wetland communities but not intact ones.

Brachiaria decumbens usually establishes too slowly to be a serious weed

in annual crops in the region, and its capacity to invade intact natural communities is negligible. However, it aggressively invades lawns, parks, roadsides, and cultivated pastures, wherever it is well adapted. It can be a serious nuisance in perennial pastures in which other species are preferred—dairy pastures, for instance—because of its progressive encroachment over a long period. *Brachiaria humidicola* parallels *B. decumbens* as an invader within its own range of adaptation, but has so far escaped attention in this respect.

Conclusions

Brachiaria species play an important role in farming systems in Asia, Australia, and the South Pacific. Their popularity can be attributed to their aggressiveness and resilience, which enable them to persist under management conditions that are less than ideal, yet they also can respond to good management. The area to which *Brachiaria* species are adapted is relatively small in Australia, but there is potential for increasing the current areas of *Brachiaria* in Asia and, to a lesser extent, in the South Pacific.

Acknowledgments

We thank the many researchers who shared their experience of *Brachiaria* species with us.

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To save space, the following acronyms are used in place of publishers' names:

ACIAR = Australian Council for International Agricultural Research

AIDAB = Australian International Development and Assistance Bureau

CSIRO = Commonwealth Scientific and Industrial Research Organisation

FAO = Food and Agriculture Organization of the United Nations

MARDI = Malaysian Agricultural Research and Development Institute

MSAP = Malaysian Society of Animal Production

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Chapter 18

Reports of Working Groups

Compiled by J. W. Miles,* B. L. Maass,* and C. B. do Valle**

Introduction

During workshop discussions, questions arose that were subsequently addressed by working groups. The questions were organized around four themes: (1) genetic resources; (2) cultivar development and adoption; (3) genetics, breeding, and biotechnology; and (4) productivity of *Brachiaria*-based pastures.

The working groups, whose reports are summarized below, were requested to discuss the status of their theme, identify constraints, outline research priorities for *Brachiaria*, recommend necessary actions, and provide a list of potential collaborators.

Group 1. Genetic Resources

Taxonomy

Status. No global revision of the genus *Brachiaria* exists, nor is there a comprehensive key to the species. *Brachiaria* is not yet organized into subgenera. Although a descriptive database on features of species and their geographic distribution is held at the Royal Botanic Gardens, Kew, Surrey, UK, it does not operate at the level of the Geographic Information Systems (GIS).

Constraints. Some species were not easy to group in the review presented at the workshop, for instance, *B. arrecta*, *B. mutica*, and *B. subquadripara*. The identity of some species (e.g., *B. distachya*, *B. miliiformis*, and *B. subquadripara*) is problematic, and some intermediates occur.

Research priorities. The genus *Brachiaria* needs a critical taxonomic review that includes geographical and environmental data, and special attention to species with potential for commercial use.

Studies on a core collection of *Brachiaria* species at the molecular level should be integrated into this review.

A reduced taxonomic key should be developed, with emphasis on species of agronomic importance.

Potential collaborators. The Royal Botanic Gardens, if funding were available, would require 2-3 years for a taxonomic review. Other collaborators may be national and regional herbaria, such as those in Nairobi, Kenya (which has a wide range of collections from East Africa), and Lisbon, Portugal (which has collections from Angola and Mozambique).

Nomenclature

Status. Some species are often not referred to by their botanically accepted names (e.g., *B. dictyoneura* cv. Llanero, which is in fact *B. humidicola*); released cultivars have sometimes been given their Latin name as their common name, for instance, *B. humidicola* cv. Humidícola in Colombia.

Constraints. Released cultivars may be taken as the typical representatives of the species. Published information available may be ignored or misinterpreted because the material worked with has been misidentified.

Recommended action. A permanent consultancy on matters related to nomenclature should be established for CIAT. Collaborators could

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be educated on nomenclature via the journal, *Pasturas Tropicales*, and CIAT staff via internal seminars.

Potential collaborators. The Royal Botanic Gardens for grasses.

Existing ex situ collections

Status. Major collections existing ex situ, documented by Keller-Grein et al. in Ch. 2, this volume, total about 1,000 accessions across institutions.

Constraints. Some species are not well represented. Sexual accessions of *Brachiaria* are little represented, and sampling methods applied to apomictic species have been inadequate. Knowledge of the agronomic potential of species other than those widely used is deficient. Some areas, for example, Rwanda and Burundi, are threatened by genetic erosion; others—such as Angola and Mozambique—inadequately collected.

Research priorities. Sexual material should be particularly sought, for example, in *B. brizantha*, and in the *B. humidicola/B. dictyoneura* complex. Sampling methodology has to be adjusted to apomictic species, based on studies on distribution of diversity. We lack knowledge of variability in some widely used species (e.g., *B. arrecta*, *B. mutica*), because ex situ collections are not available. Little-known species with agronomic potential should be collected; for instance, *B. subquadripara* (*B. miliiformis*) for shade tolerance and *B. ambigens* for semiarid areas. The literature should be thoroughly searched for little-known species with forage value. Additional collections of *Brachiaria* could be made from areas where other genera are being collected.

Potential collaborators. It is important to collaborate with national institutions, particularly in Africa. The help of the Institut français de recherche scientifique pour le développement en coopération (ORSTOM), based at the ICRISAT Sahelian Center, should be enlisted to collect *Brachiaria* in semiarid areas. Other possible collaborators are the International Livestock Research Institute (ILRI), both Ethiopia and Kenya, and the International Plant Genetic Resources Institute (IPGRI).

Conservation of germplasm

Conservation ex situ. The largest collections of *Brachiaria*, at CIAT and ILRI, Ethiopia, are both maintained mainly as field collections. However, much of the material has not yet been duplicated; only a few accessions are conserved by good quality seed; and large portions of collected materials have been lost from several major ex situ collections.

Constraints. Neither seed storage nor techniques for in vitro movement of germplasm are reliable. No protocol exists for in vitro conservation.

Research priorities. High priority should be given to duplicating every *Brachiaria* accession. Research is needed on seed physiology and storage, including dormancy, and on in vitro methods of conservation.

Potential collaborators. Potential collaborators in germplasm conservation include the Royal Botanic Gardens, for seed physiology; the University of Reading, UK; and the International Seed Testing Association (ISTA). More coordination is needed within the Network of Tropical and Subtropical Forage Genetic Resources, national and regional gene banks, such as the Centro Nacional de Recursos Genéticos e Biotecnologia (CENARGEN) and the Genebank of Kenya (GBK). Training could be given by IPGRI.

Conservation in situ. Some inventories of national parks do exist; however, no particular information is available on genetic erosion of *Brachiaria*.

Constraints. Lack of knowledge is the principal constraint to germplasm conservation in situ.

Research priorities. The ecological status of species in East African national parks should be monitored at regular intervals. *Brachiaria* species in the Kitale collection should be collected again; this would enable monitoring of existing *Brachiaria* populations.

Potential collaborators. National parks, environmental organizations, universities, herbaria, and the GBK would all be potential collaborators in this venture.

Characterization and documentation

Status. At CIAT, biochemical, morphological, and reproductive mode characterization have been accomplished, and almost all materials identified. However, some confusion still exists over the identity of accessions among different genetic resources centers. Many accessions have herbarium specimens from the original collection site.

Constraints. The main constraint to characterization and documentation of *Brachiaria* accessions is our lack of understanding of geographic patterns of genetic diversity.

Recommended action. Voucher specimens should be taken from collection sites and multiplication sites if vegetatively increased in the country of origin. High priority should be given to revising the documentation of collection and to identifying accessions. A comprehensive germplasm catalog should be published within a year. Further data analysis (morphology, isozymes, reproductive mode, and geographic and environmental information on collection sites) should be formatted to a GIS database.

Potential collaborators. Potential collaborators in this area could be ILRI (Ethiopia) for documentation and both ILRI (Ethiopia) and CNPGC/EMBRAPA for morphological characterization. Work could be coordinated through the Network of Tropical and Subtropical Forage Genetic Resources.

Group 2. Cultivar Development and Adoption

Attributes needed in new cultivars of *Brachiaria*

Status. Six commercial cultivars of *Brachiaria* have been adopted and are planted on millions of hectares, primarily in tropical America.

Constraints. All existing commercial cultivars have one or more recognized defects that limit their usefulness, productivity, or persistence.

Research priorities. Attributes needed in new cultivars of *Brachiaria* should be clearly and objectively defined. The Working Group defined these attributes as follows:

Ecology.

1. Broad ecological adaptability with respect to climate, soil (low pH, low P, poor drainage), and topography (elevation, slope);
2. Ease of establishment, with high percentage of germination, vigorous seedling growth, and fast soil cover;
3. Efficient weed suppression;
4. Compatibility with associated legumes;
5. Persistence under grazing;
6. Shade and fire tolerance;
7. Adaptability to different grazing management regimes (and mismanagement).

Seed production.

1. Ability to produce abundant supplies of good quality seed;
2. Intermediate level of seed dormancy (comparable with cv. Basilisk).

Productivity.

1. Forage quality: (a) digestibility of energy and protein, balanced

mineral content; (b) freedom from toxins—oxalates and saponins—that cause photosensitization and other symptoms in livestock; (c) seasonal maintenance of forage quality.

2. Forage quantity: (a) high gross annual DM yield; (b) good seasonal distribution through cool and/or dry season.
3. Pest and disease resistance: (a) to spittlebugs, (b) to *Rhizoctonia*, rust, and ergot.

Evaluation methods

Status. Large collections are evaluated in the field for general climatic, edaphic, and biotic constraints; this is followed by evaluation in the greenhouse for spittlebug resistance, response to fertilizer, and quality. Regional cutting trials are then conducted, followed by regional grazing trials.

Constraints. In breeding programs that use large quantities of material, methods of evaluating for spittlebug resistance are imprecise. Organization of procedures, site choice, and flow of information are inadequate. Mechanisms of edaphic adaptation are not understood well enough to allow quick measurement. Evaluation of digestibility in the large germplasm pool is inadequate.

Research priorities. Research should focus on understanding mechanisms of spittlebug resistance and of edaphic adaptation in *Brachiaria*. The international flow of information on evaluation needs improving.

Release mechanisms

Status. Mechanisms and procedures for releasing new cultivars differ by country; very few countries have official release authorities.

Constraints. The time and cost of gathering data on animal production are too high to allow adequate coverage of various ecosystems. Besides, no consensus exists on the methodology most appropriate for grazing trials. International coordination and facilitation are needed. Animal performance on a particular candidate to cultivar status should be evaluated before release.

Adoption

Status. New cultivars are usually readily adopted; an exception was the initial slow adoption of cv. La Libertad in Colombia after its release.

Constraints. Successful adoption depends on the availability of cheap and plentiful commercial seed, promotional activities, and availability of technical information.

Recommended action. Mechanisms should be sought to involve the private seed sector in the final stages of prerelease research and seed multiplication.

Group 3. Genetics, Breeding, and Biotechnology

Knowledge base

Status. Basic knowledge is becoming available on genetics, breeding methods, and biotechnology tools to support productive applied breeding programs for *Brachiaria*.

Constraints. Our knowledge of the genetics and of the expression of traits of agronomic importance is inadequate. No compatible sexual biotype exists in the *B. humidicola* complex. We lack transformation protocols. Present breeding schemes are entirely empirical and lack a solid theoretical basis. We also lack simple, fast, and efficient screening techniques for major traits, such as spittlebug resistance.

Research priorities. Efficient breeding schemes, based on quantitative genetic analysis, should be developed to exploit apomixis. Reliable and fast techniques should be developed for

assessing reproductive mode and spittlebug resistance. Biotechnology tools (molecular markers, transformation protocols) should be used to improve efficiency of screening for superior genotypes. A compatible sexual should be found or created to overcome the apomixis barrier in the *B. humidicola*/*B. dictyoneura* group. Development of a mechanism to control expression of apomixis (i.e., to achieve sexual reproduction in a genetically apomictic biotype) would be extremely useful in *Brachiaria* breeding.

Role of the private sector

Status. Brazil dominates the forage seed market, with government organizations evaluating and transferring seed to the Basic Seed Foundation, which organizes subsequent multiplication and release through private companies. Private sector promotion has a stronger influence than government extension on adoption of new cultivars; therefore, the involvement of the Brazilian seed industry is vital for promoting new cultivars throughout tropical America.

Constraints. The main constraint to more active involvement of the private sector is the absence of legal mechanisms and procedures.

Recommendations. Legal mechanisms for release procedures need to be worked out between the government and private sector. Better linkages should be developed between the private sector—which has information on what attributes are needed in new cultivars and could sponsor regional trials—and research organizations, which could benefit from this information and expand evaluation over several sites.

Group 4. Productivity of *Brachiaria*-based Pastures

Germplasm

Status. *Brachiaria decumbens* cv. Basilisk is the most widely planted cultivar in the savannas and the humid tropics.

Constraints. A major constraint of cv. Basilisk, especially in the humid tropics, is its susceptibility to spittlebugs. Its dry-season performance limits production, especially in the Brazilian Cerrados. The spittlebug-resistant cultivar, *B. brizantha* cv. Marandu, is not adapted to infertile soils and long dry seasons. Cultivars with good edaphic adaptation (e.g., commercial *B. humidicola* and *B. dictyoneura* cv. Llanero) have lower forage quality and are also good hosts for spittlebugs.

Research priorities. Future research on germplasm should focus on spittlebug resistance; edaphic adaptation with associative N_2 fixation, combined with high forage quality; drought and shade tolerance; high and reliable seed production; and tolerance of poor drainage.

Pasture degradation

Status. We have a lot of anecdotal information but limited research data on pasture degradation. In the savannas, the main cause of pasture degradation is low soil fertility, especially lack of P, followed by lack of other nutrients (N, K, and Ca). In the humid tropics, pasture degradation results from soil compaction, spittlebug infestation, and runoff of nutrients. Lack of legumes in the pasture system and inadequate management (overgrazing, lack of maintenance fertilizer, burning) further contribute to degradation of *Brachiaria* pastures.

Research priorities. Multilocational trials should be conducted at contrasting sites to determine the mechanisms involved in pasture degradation, using a range of cultivars and management strategies.

Pasture reclamation

Status. Farmers are using different methods of reclaiming degraded pastures: mechanical cultivation, often combined with fertilizer application; burning and reseeding; and crop rotation.

Constraints. In the long term, grass monocultures, without associated legumes, constrain productivity. The long-range effect of these systems on pasture and soil quality has not been defined.

Research priorities. Suitable legumes should be identified for growing in association with *Brachiaria* in short- and long-term pastures. The effects of current pasture reclamation systems on pasture productivity and soil quality should be quantified.

Potential collaborators.
Germplasm development: EMBRAPA (CNPAB, CNPGC, CPAC), CIAT.

Pasture degradation: CIAT, EMBRAPA (CNPAB, CNPGC, CPAC), MARDI, CORPOICA, IVITA/INIAA.

Pasture reclamation: EMBRAPA (CNPAF, CNPGC, CPAC, CPATU), IVITA/INIAA, CORPOICA, MARDI.

Photosensitization and toxicity: EMBRAPA (CNPGC), FONAIAP, CIAT, MARDI, UPM.[1]

1. For full names of institutions, see "Appendix: Acronyms and Abbreviations," p. 283.

Chapter 19

A Summing Up

J. W. Miles*

This was a comprehensive workshop, touching on topics ranging from taxonomic classification within a genus that occurs throughout the tropics to the adaptation and utility of existing *Brachiaria* cultivars in regional production systems.

We have learned something of *Brachiaria*'s phylogenetic diversity, which extends far beyond the handful of species for which we currently recognize agricultural potential. These fall into only two of the nine taxonomic groups proposed for the genus. I believe that taxonomists will recognize the inadequacy of the tentative classification proposed and the need for a more biologically meaningful classification, based on much greater use of modern molecular criteria of classification.

In the past 10 years, a reasonably large collection of *Brachiaria* germplasm has been assembled, and preliminary agronomic evaluation of this is now nearing completion. Its usefulness as a source of desirable attributes for breeding work has already been shown. But a question still remains as to whether this collection will be the direct source of useful new commercial cultivars. The advisability of additional collection to broaden both the taxonomic and the geographic coverage was debated.

Morphological, biochemical, and molecular characterization of our collection has begun, and this exercise will yield useful information regarding relationships among species and the organization of genetic diversity within species.

A rigorous study of the physiology of even the few commercially important *Brachiaria* species is lacking. Our knowledge of the most basic attributes, such as flowering responses to temperature and photoperiod, from which one might infer appropriate seed production environments, is at present entirely empirical.

We have a considerable body of evidence regarding edaphic adaptation of the commercial *Brachiaria* biotypes. However, a clear delineation of the soil properties that constrain adaptation, and detailed studies of the underlying plant physiological mechanisms controlling this adaptation—from which we may hope to identify better adapted genotypes—are only beginning to be known.

Because of the vast land areas covered by sown *Brachiaria* pastures in tropical America, their potential ecological impact must be considered. Because they provide permanent soil cover, are deep-rooted, and fix significant amounts of biological N, well-managed *Brachiaria* pastures have an important positive impact on the environment, particularly if they are associated with a well-adapted, persistent forage legume, such as *Arachis pintoi*.

Even though they are essentially monocultures covering millions of hectares in tropical America, *Brachiaria* pastures are notably free from insect pests and diseases, their most significant biotic constraint being several species of spittlebug. Refinement of screening methods and elucidation of the mechanisms of host-plant resistance should lead to the development of cultivars that combine spittlebug resistance with other needed attributes.

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Compared with other tropical forage grasses, the forage quality of existing cultivars of *B. decumbens* and *B. brizantha* is good. Substantial scope for further genetic improvement in digestibility has now been documented.

We know very little of the physiological factors involved in *Brachiaria* seed production and quality. Experience, mainly accumulated by the private seed sector, has helped identify appropriate production areas and seed-crop management practices that allow high yields of good quality seed at acceptable cost.

Over the past 20 years, a vigorous private forage-seed industry has developed in Brazil: at first, to satisfy internal demand, which had previously been met from Australia, and later, to meet a growing demand for *Brachiaria* seed throughout tropical America. This private seed sector, supported in large part by sales of *Brachiaria* seed, has a legitimate and vital interest in public sector research and development of new *Brachiaria* forage grasses.

Major advances have been made in the past decade in understanding the cytology, genetics, and reproductive behavior of *Brachiaria* species. This knowledge provides the essential underpinnings of recent plant breeding initiatives in the genus.

Viable applied breeding programs are now under way in Brazil and Colombia. We have made considerable progress toward full control of apomixis in our quest for improved *Brachiaria* cultivars that combine desirable attributes not found in the collections of natural germplasm.

Biotechnology holds promise in the genetic manipulation of crops, and many techniques are now available to assist the plant breeder. Advances have been greater in crops with a long tradition of genetic improvement than in *Brachiaria*, where plant breeding is a recent activity.

Relevant biotechniques are already being applied to the special challenges of breeding an apomictic forage grass. These include molecular marker technology, which is teaching us much about the genetic control of apomixis and may eventually permit more precise manipulation of reproductive mode in *Brachiaria* breeding.

Brachiaria is not the solution to all needs for livestock feed. Perhaps ironically, *Brachiaria* species as cultivated pastures appear to have only limited utility in their native Africa. This is not because of defects in adaptation, as in the case of *Stylosanthes* cultivars, which were selected in Australia, reintroduced into their native tropical America, and devastated by the endemic anthracnose disease. In contrast, *Brachiaria* species, whether native or reintroduced, are productive and appear notably free from disease or insect attack in Africa. But they lack an appropriate niche in the prevailing livestock production systems, where extensive grazing on large private ranches simply does not exist.

In Southeast Asia, *Brachiaria* is finding a significant and growing niche in prevailing production systems. But it is in tropical America, particularly on infertile acid soils, that the *Brachiaria* grasses realize their greatest potential and are of such tremendous economic (as well as ecological) significance. Here, they provide both persistent and sustainable vegetative cover in deforested areas of the humid tropics, and substantially increase animal production potential on the vast tropical American savannas, primarily in Brazil, Colombia, and Venezuela.

The full biological and commercial potential of this tropical grass genus is only beginning to be recognized. Our hope is that this volume will be a useful contribution to the realization of this potential.

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Appendix

Acronyms and Abbreviations

Acronyms

AAB	Association of Applied Biologists, UK
ACIAR	Australian Centre for International Agricultural Research
AFRNET	African Feed Resources Network, *coordinated by* ILRI
AGROSSCA	Agropecuaria de Semillas y Servicios S.A., Venezuela
AIDAB	Australian International Development and Assistance Bureau
APONET	International Network for Apomixis Research
ARC	African Research Council, South Africa
ARNAB	African Research Network for Agricultural Byproducts, *coordinated by* ILRI
ARS	Agriculture Research Service of USDA
ASA	American Society of Agronomy
ASAP	Australian Society of Animal Production
ATFGRC	Australian Tropical Forages Genetic Resources Centre of CSIRO
CA	Département des cultures annuelles of CIRAD, *formerly* IRAT
CAB	Commonwealth Agricultural Bureaux, *now* CAB International
CAB International	Centre for Agriculture and Biosciences International, *formerly* CAB
CATI	Coordenadoria de Assistência Técnica Integral, Brazil
CATIE	Centro Agronómico Tropical de Investigación y Enseñanza, Costa Rica
CENARGEN	Centro Nacional de Recursos Genéticos e Biotecnologia of EMBRAPA
CENIAP	Centro Nacional de Investigaciones Agropecuarias of FONAIAP
CEPEC	Centro de Pesquisas do Cacau, Brazil
CEPLAC	Comissão Executiva do Plano da Lavoura Cacaueira, Brazil
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo, Mexico
CIRAD	Centre de coopération internationale en recherche agronomique pour le développement, France
CMI	Commonwealth Mycological Institute of CAB, *now* IMI of CAB International
CNPAB	Centro Nacional de Pesquisa de Agrobiologia of EMBRAPA
CNPAF	Centro Nacional de Pesquisa de Arroz e Feijão of EMBRAPA
CNPBS	Centro Nacional de Pesquisa de Biologia do Solo of EMBRAPA
CNPGL	Centro Nacional de Pesquisa de Gado de Leite of EMBRAPA
CNPMF	Centro Nacional de Pesquisa de Mandioca e Fruticultura, *formerly* IPEAL, of EMBRAPA
CORPOICA	Corporación Colombiana de Investigación Agropecuaria, Colombia

CPAC	Centro de Pesquisa Agropecuária dos Cerrados of EMBRAPA
CPATU	Centro de Pesquisa Agropecuária do Trópico Úmido, *formerly* IPEAN, of EMBRAPA
CRECED	Centros Regionales de Capacitación, Extensión y Difusión de Tecnología, Colombia
CSIR	Council for Scientific and Industrial Research, *now* CSIRO
CSIRO	Commonwealth Scientific and Industrial Research Organisation, *formerly* CSIR, Australia
CSSA	Crop Science Society of America
DIEAF	Dirección de Investigación y Extensión Agropecuaria y Forestal of MAG, Paraguay
EBDA	Empresa Baiana de Desenvolvimento Agrícola S.A., Brazil
EEPFIH	Estación Experimental de Pastos y Forrajes "Indio Hatuey," Cuba
EMCAPA	Empresa Capixaba de Pesquisa Agropecuária of EMBRAPA
EMGOPA	Empresa Goiana de Pesquisa Agropecuária, Brazil
EMVT	Département d'élevage et de médicine vétérinaire of CIRAD, *formerly* IEMVT
EPAMIG	Empresa de Pesquisa Agropecuária de Minas Gerais, Brazil
ESALQ	Escola Superior de Agricultura "Luiz de Queiroz" da Universidade de São Paulo, Brazil
ESSUL	Estação de Zootecnia do Extremo Sul da Bahia of CEPLAC
ETES	Estudio Técnico y Económico de Sistemas de Producción Pecuaria, Brazil, Colombia, and Venezuela
FAO	Food and Agriculture Organization of the United Nations, Italy
FAPESP	Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil
FEALQ	Fundação de Estudos Agrários "Luiz de Queiroz," Brazil
FIBGE	Fundação Instituto Brasileiro de Geografia e Estatística, Brazil
FLFAM	Federal Livestock Farmer Association of Malaysia
FONAIAP	Fondo Nacional de Investigaciones Agropecuarias, Venezuela
FUNEP	Fundação de Estudos e Pesquisas em Agronomia, Medicina Veterinaria e Zootecnia, Brazil
GBK	Genebank of Kenya
IAC	Instituto Agronómico de Campinas, Brazil
IAPAR	Fundação Instituto Agronómico do Paraná, Brazil
IAR	Institute of Agricultural Research, Ethiopia
IBPGR	International Board for Plant Genetic Resources, *now* IPGRI
ICA	Instituto Colombiano Agropecuario
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics, India
IDIAP	Instituto de Investigación Agropecuaria de Panamá
IEMVT	Institut d'élevage et de médicine vétérinaire des pays tropicaux of CIRAD, *now* EMVT

IGER	Institute of Grassland and Environmental Research, UK
IICA	Instituto Interamericano de Cooperación para la Agricultura, Costa Rica
IIPF	Instituto de Investigaciones de Pastos y Forrajes, Cuba
IITA	International Institute of Tropical Agriculture, Nigeria
ILCA	International Livestock Centre for Africa, *now* ILRI, Ethiopia
ILRAD	International Laboratory for Research on Animal Diseases, *now* ILRI, Kenya
ILRI	International Livestock Research Institute, *created from merger of* ILCA and ILRAD, Ethiopia and Kenya
IMI	International Mycological Institute, *formerly* CMI, of CAB International
INEAC	Institut national pour l'étude agronomique du Congo Belge
INIA	Instituto de Investigaciones Agropecuarias, Chile
INIA	Instituto Nacional de Investigaciones Agrícolas, Mexico, *now* INIFAP
INIA	Instituto Nacional de Investigación Agraria, Peru
INIAA	Instituto Nacional de Investigación Agraria y Agroindustrial, *now* INIA, Peru
INIAP	Instituto Nacional de Investigaciones Agropecuarias, Ecuador
INIFAP	Instituto Nacional de Investigaciones Forestales y Agropecuarias, *formerly* INIA, Mexico
INRA	Institut national de la recherche agronomique, France
IPEAL	Instituto de Pesquisas e Experimentação Agropecuárias do Leste, *now* CNPMF
IPEAN	Instituto de Pesquisas e Experimentação Agropecuárias do Norte, *now* CPATU
IPGRI	International Plant Genetic Resources Institute, *formerly* IBPGR, Italy
IRAT	Institut de recherches agronomiques tropicales et des cultures vivrières of CIRAD, *now* CA
IRI	Instituto de Pesquisas IRI, Brazil
IRI	IBEC Research Institute, *now* IRI Research Institute, Inc., New York, USA
IRRI	International Rice Research Institute, Philippines
IRZ	Institut de recherches zootechniques, Cameroon
ISABU	Institut des sciences agronomiques du Burundi
ISTA	International Seed Testing Association, Switzerland
IVITA	Instituto Veterinario de Investigaciones Tropicales y de Altura, Peru
JSGS	Japanese Society of Grassland Science
MAARA	Ministério da Agricultura, do Abastecimento e da Reforma Agrária, Brazil
MAC	Ministerio de Agricultura y Cría, Venezuela
MAG	Ministerio de Agricultura y Ganadería, Costa Rica
MAG	Ministerio de Agricultura y Ganadería, Paraguay
MARDI	Malaysian Agricultural Research and Development Institute
MSAP	Malaysian Society for Animal Production
NZGA	New Zealand Grassland Association

NZIAS	New Zealand Institute of Agricultural Science
NZSAP	New Zealand Society of Animal Production
ORSTOM	*formerly* Office de la recherche scientifique et technique d'outre-mer, *now* Institut français de recherche scientifique pour le développement en coopération, France
PANESA	Pasture Network for Eastern and Southern Africa
PESAGRO	Empresa de Pesquisa Agropecuária do Estado do Rio de Janeiro
PRONIEGA	Programa Nacional de Investigación y Extensión Ganadera of MAG, Paraguay
QDPI	Queensland Department of Primary Industries, Australia
RABAOC	Réseau de recherche en alimentation du bétail en Afrique Occidentale et Centrale (West and Central African Feed Research Network), *coordinated by* CIAT, EMVT, *and* AFRNET
RBG	Royal Botanic Gardens, Kew, UK
RGI	*formerly* Roodeplaat Grassland Institute, *now* Range and Forest Institute, of the ARC
RIEPT	Red Internacional de Evaluación de Pastos Tropicales (International Tropical Pastures Evaluation Network), *coordinated by* CIAT
SARH	Secretaría de Agricultura y Recursos Hidráulicos, Mexico
SBZ	Sociedade Brasileira de Zootecnia, Brazil
SCJ	Science Council of Japan
SEAFRAD	Southeast Asian Forage Research and Development Network, *coordinated by* CIAT *and* CSIRO
SSSA	Soil Science Society of America
TGSA	Tropical Grasslands Society of Australia
UCV	Universidad Central de Venezuela
UEPAE	Unidade de Execução de Pesquisa de Âmbito Estadual of EMBRAPA
UFRRJ	Universidade Federal Rural do Rio de Janeiro, Brazil
UNESCO	United Nations Educational, Scientific, and Cultural Organization, France
UNICAMP	Universidade Estadual de Campinas, Brazil
UPM	Universiti Pertanian Malaysia
USDA	United States Department of Agriculture

Abbreviations

2,4-D	2,4-dichlorophenoxyacetic acid (medium)
ACP	αβ-acid phosphatase
A.C.T.	Australian Capital Territory
AD	apparent density (of soils)
ADH	alcohol dehydrogenase
AFLPs	amplified fragment length polymorphisms (genetics)
an.	animal
APO	apomictic mode of reproduction (in plants)
AU	animal unit
BA	Bahia, state of Brazil
BC	backcross (in genetics)
BNF	biological nitrogen fixation
bri	*Brachiaria brizantha*
bt	*Bacillus thuringiensis* gene
CaMV	cauliflower mosaic virus
cat	chloramphenicol acetyltransferase (reporter gene)
cDNA	complementary DNA
CEC	cation exchange capacity
Ch.	Chapter
CP	crude protein
cv.	cultivar
DC	direct current (electricity)
DDM	in vivo digestible dry matter
dec	*Brachiaria decumbens*
DIA	diaphorase
DM	dry matter
DNA	deoxyribonucleic acid
ES	Espírito Santo, state of Brazil
ESA	embryo-sac analysis
EST	α-, β-esterase
FISH	fluorescent in situ hybridization
FS	full-sib mating
GIS	Geographic Information Systems
GO	Goiás, state of Brazil
GOT	glutamate oxaloacetate transaminase
G6PDH	glucose-6-phosphate dehydrogenase
gus	β-glucuronidase (reporter gene)
GxE	genotype-by-environment interaction
hd	head (of cattle)
HS	half-sib mating
ISH	in situ hybridization
IVDMD	in vitro dry matter digestibility
lux	bacterial or firefly luciferase (reporter gene)
LWG	liveweight gain
MDH	malate dehydrogenase
ME	malic enzyme
MG	Minas Gerais, state of Brazil
mRNA	messenger RNA
MS	Mato Grosso do Sul, state of Brazil
MS	Murashige and Skoog medium
NAA	α-naphthylacetic acid
NARS	National agricultural research systems
NDF	neutral detergent fiber (cell-wall content of pasture plants)
nos	nopaline synthase promoter
npt11	neomycin phosphotransferase (gene)
OM	organic matter
PA	Pará, state of Brazil
PARP	partially acidulated rock phosphate
PCA	principal component analysis (statistics)
PCR	polymerase chain reaction (genetics)
PEG	polyethylene glycol
PEP-CK	phosphoenolpyruvate carboxykinase
pH	symbol for the degree of acidity or alkalinity of a solution
PLS	pure live seed
PRINS	primed in situ hybridization
PRX	peroxidase
PT	progeny test
Qld.	Queensland, state of Australia
QTLs	quantitative trait loci (genetics)
RAPD	random amplified polymorphic DNA (genetics)
RFLPs	restriction fragment length polymorphisms (genetics)
RGI	relative growth index; *also* dry-to-wet season growth ratio
RJ	Rio de Janeiro, state of Brazil
RLD	root length density
RNA	ribonucleic acid
RM	reproductive mode
RO	Rondônia, territory of Brazil
ruzi	*Brachiaria ruziziensis*

SCARs	sequence characterized amplified regions (genetics)
SEX	sexual mode of reproduction (in plants)
SKDH	shikimate dehydrogenase
SP	São Paulo, state of Brazil
SSP	single superphosphate
T-DNA	tumor-inducing DNA
TRF	tropical rain forest
TSSF	tropical semievergreen seasonal forest
UPGMA	unweighted pair-group method arithmetic average (statistics)
V	volt
VAM	vesicular-arbuscular mycorrhizae
Vic.	Victoria, state of Australia
VNTRs	variable number tandem repeats (genetics)
WHC	water-holding capacity (of soil)
WSMT	wet-season mean temperature
WSPE	total wet-season potential evapotranspiration
YACs	yeast artificial chromosomes

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