HOST PLANT RESISTANCE TO WHITEFLIES WITH EMPHASIS ON CASSAVA AS A CASE STUDY

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Abstract

Host plant resistance (HPR) to whiteflies is rare in cultivated crops. A literature search revealed that HPR research with the *Bemisia tabaci*/*B. argentifolii* complex has increased considerably in recent years, but large-scale screening of a wide selection of genotypes is limited. At the International Center for Tropical Agriculture (CIAT) in Colombia, more than 5000 cassava clones have been evaluated for resistance to *Aleurotrachelus socialis*. Several cultivars with high levels of resistance have been identified. Nymphal mortality was highest on the resistant cassava clone, M Ecu 72 (72.5%) and lowest on the susceptible clones CMC 40 (33%) and M Bra 12 (25.0%). When feeding on resistant genotypes, *A. socialis* had less oviposition, longer development periods, reduced size and higher mortality than when feeding on susceptible ones. Mortality is highest during the Nymphal stages. Several whitefly resistant hybrids have been developed using M Ecu 72 as the resistant female parent. Three hybrids are being evaluated for release by the Colombian Ministry of Agriculture and Rural Development.

Keywords: Cassava, *Aleurotrachelus socialis*, *Bemisia tabaci, Bemisia argentifolii*, resistant genotypes, AFLP

1. Introduction

Whiteflies are considered one of the world's major agricultural pest groups, attacking a wide range of crop hosts and causing considerable crop loss. As direct-feeding pests and virus vectors, whiteflies cause major damage in agroecosystems based on cassava (Euphorbiaceae: *Manihot esculenta* Crantz) in the Americas, Africa and, to a lesser extent, in Asia. The largest complex of whitefly pests on cassava is found in the Neotropics, where 11 species are reported. The most important species include *Aleurotrachelus socialis* Bondar, *Trialeurodes variabilis* (Quaintance), *Bemisia tuberculata* Bondar, *B. tabaci* (Gennadius), *B. argentifolii* Bellows and Perring, and

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Aleurothrixus aepim (Goldi) (Bellotti *et al.*, 1999). *A. socialis* and *A. aepim* cause considerable direct-damage yield losses in northern South America and Brazil. *A. socialis* appears specific to cassava (no additional hosts have been identified) and predominates in Colombia, Venezuela and Ecuador. *A. aepim*, which primarily attacks cassava but has other hosts, is found in high populations, causing yield losses in Northeast Brazil (Farias, 1990, 1994). *B. tabaci*, the vector of African Cassava Mosaic Disease (ACMD) has a pantropical distribution, feeding on cassava throughout Africa, several countries in Asia and more recently in the Neotropics. ACMD is caused by several geminiviruses (Thresh *et al.,* 1994), and it has been speculated that the absence of ACMD in the Americas may be related to the inability of its vector, *B. tabaci*, to colonize cassava. Prior to the early 1990s the *B. tabaci* biotypes found in the Americas did not feed on cassava (Costa and Russell, 1975; Wool *et al*., 1994).

Since the early 1990s a new biotype (B) of *B. tabaci*, considered by some to be a separate species (*B. argentifolii*), has been found feeding on cassava in the Neotropics. Although ACMD has not been reported from the Americas, it is considered that ACMD now poses a more serious threat to cassava production as most traditional cultivars in the region are highly susceptible to the disease. In addition the *B. tabaci* biotype complex is the vector of viruses on several other crops often grown in association with cassava or near it (e.g. beans, cowpeas, sweet potatoes, string beans, tomatoes, cotton). The possibility of viral diseases moving among these crops or the appearance of new viruses represents a potential threat, e.g. tomato yellow leaf curl virus infecting common bean (Navas-Castillo, *et al*., 1999).

Whiteflies, especially in the Neotropics, cause direct damage to cassava by feeding on the phloem of the leaves. This causes symptoms such as chlorosis and leaf fall, which result in considerable reduction in root yield if prolonged feeding occurs. Yield losses resulting from *A. socialis* and *A. aepim* activity (Vargas and Bellotti, 1981, Bellotti *et al.*, 1999, Farias, 1990) are common in Colombia and Brazil. In the case of *A. socialis* feeding, there is a correlation between duration of attack and yield loss. Infestations of 1, 6 and 11 months resulted in a 5, 42 and 79% yield reduction, respectively (Vargas and Bellotti, 1981).

Host plant resistance (HPR) offers a low-cost, practical, long-term solution for maintaining lower whitefly populations and reducing crop losses. This is especially important for crops such as cassava, which has a long growing cycle (1 year or more) and is most often grown by resource-limited smallholder farmers who cannot afford costly inputs.

HPR studies for whitefly resistance in cassava were initiated at the International Center for Tropical Agriculture (CIAT) more than 15 years ago. Systematic evaluation of the cassava germplasm bank has resulted in identifying several *A. socialis*-resistant cultivars. The situation in cassava, where high levels of resistance to the whitefly species A. *socialis* have been observed in cassava germplasm, is unique. This paper describes the process of varietal screening and evaluation, and the development of hybrids combining resistance and agronomic value. The cassava case can serve as a model for evaluating germplasm collections and developing HPR in other crops attacked by whiteflies. Host plant resistance breeding for whitefly transmitted geminiviruses is reviewed in this volume by Morales (2001).

2. Whitefly Resistance in Cultivated Crops

HPR to whiteflies is rare in cultivated plants. The large-scale screening or evaluation of an extensive collection of cultivars, breeding materials, hybrids or selected wild or cultivated species for whitefly resistance has been limited (De Ponti *et al*., 1990). In many cases the range of germplasm evaluated is too limited to understand or obtain the diversity of whitefly-resistance genes that may be available in a given crop species.

A literature search identified only a few deliberate development programs to identify and select resistant parental genotypes, to combine genotypes of high agronomic value and to produce cultivars with resistance to whiteflies. Whitefly HPR research has increased considerably since 1990, primarily due to the rise in importance and damage caused by the *B. tabaci* species complex. This species complex feeds on a wide range of crops, causing yield losses due to direct-feeding damage and as vectors of numerous geminiviruses (De Ponti *et al*., 1990; Brown *et al*., 1996, Drost *et al*., 1998). In addition HPR studies have also been carried out with other whitefly species including *Trialeurodes abutilonea* on soybeans (McPherson, 1996; Lambert *et al*., 1997); *Aleurothrixus aepim* on cassava in Brazil (Farias, 1990); *Bemisia afer* on cassava in Malawi (Munthali, 1992); *T. vaporariorum* on tomatoes in the Netherlands (De Ponti *et al*., 1990, Van Giessen *et al*., 1995), *T. vaporariorum* on peppers in Europe (Laska *et al*., 1986); and *Aleurotrachelus socialis* on cassava in Colombia (Bellotti *et al*., 1999).

Although HPR research on whiteflies is now being carried out in more than 15 countries, US researchers are the most active, followed by those in India, Israel and, to a lesser extent, Spain and Egypt. The range of agricultural crops being evaluated for whitefly resistance is increasing, primarily as a result of the wide host range of the *B. tabaci* species complex. Included in this list are numerous legumes [common beans (*Phaseolus vulgaris*), soybeans, mung beans, snap beans, groundnuts, alfalfa and cowpeas], cucurbits (melons, squash, cucumbers and zucchini), brassicas (cabbage, collards, broccoli), solanaceous crops (tomatoes, eggplant, tobacco and potatoes) and others (cotton and okra) (Tables 1 and 2).

A recent literature search revealed that germplasm evaluations often involve the comparison of whitefly infestations on different crops, especially with the *B. tabaci-B. argentifolii* complex. This research usually measures whitefly survival (primarily nymphs), oviposition and, to a lesser extent, crop damage. Table 1 represents an example of this type of research, usually carried out in the greenhouse and with caged plants. These studies may compare closely related crops such as squash and zucchini (McAuslane *et al*., 1996) or nonrelated species such as cotton and poinsettias (Bethke *et al*., 1991). These comparisons are often made to determine which crops might attract or sustain the highest whitefly populations. For example, it appears that zucchini, cantaloupes and cotton are most preferred, while broccoli is the least preferred (Table 1) (Blua *et al*., 1995, Costa *et al*., 1991, Chu *et al*., 1995).

There is a wide range of crop species that are now being screened for whitefly resistance. In most cases there is a limited amount of germplasm that is actually being evaluated for whitefly damage (Table 2), the emphasis being on cultivars. Table 2 represents some examples of this research reported in the recent literature, dealing only with the *B. tabaci-B. argentifolii* complex. Most are field evaluations, but greenhouse and laboratory studies are also being conducted. A visual rating

system based on plant/foliar damage is often employed to distinguish resistant or susceptible germplasm. Results from these studies are often difficult to interpret from the literature. The number of germplasm accessions selected as resistant or promising for resistance is usually very low, and reports usually refer to "less damaged" or "having low whitefly populations".

The whitefly-resistance project for alfalfa is one of the few examples that involve a deliberate breeding effort to develop high-yielding, whitefly-resistant cultivars (Teuber *et al*., 1996). These researchers have devised a breeding method among and within half-sib (a group of plants with the same female parent) family selection, where the best plants are selected from the best families based on selection criteria such as the absence of whitefly immatures and leaf stickiness. The cultivar UC Impalo WF, resistant to the silverleaf whitefly, has been released and is presently being grown on 12 to 15000 acres in the San Joaquin and Imperial Valleys of California (Teuber, personal communication).

The literature also contains reports of several crops with genotypes "resistant" to the *B. tabaci* species complex. As far as could be determined, in most cases these are not cultivars that were developed for whitefly resistance; rather they are cultivars or breeding lines that happen to contain resistance and were selected during field or greenhouse trials. In several cases antixenosis (nonpreference for oviposition or feeding) or tolerance appears to be the resistance mechanism in operation (Table 3). Glabrousness, trichome density, latex, acylsugars and glossy foliage have also been linked to resistance. Glabrous cotton cultivars resulted in lower oviposition and few nymphs (Butler *et al*., 1992, Navon *et al*., 1991), while glabrous-leafed melons (*Cucumis melo*) were found to reduce numbers of whitefly stages (adults and nymphs), when compared to commercial pubescent-leafed cultigens (Riley *et al*., 2001). Higher phenolic and odihydroxy phenolic content of cotton cultivars resulted in fewer eggs oviposited by the *Bemisia* complex (Butler *et al*., 1992), and vascular bundle depth was negatively related to *B. argentifolii* adult and nymph densities (Chu *et al*., 1998).

3. Host Plant Resistance in Cassava: A Case Study

3.1 Cassava germplasm: Evaluation for whitefly resistance

Cassava is a perennial shrub grown throughout the tropical and subtropical regions of the world. It originated and was domesticated in the Neotropics (Renvoize, 1973; Allem, 1994). The crop was introduced into Africa in the 16th century, where it is now cultivated across an extensive area, referred to as the "cassava belt." In the 17th century, cassava was introduced into Asia, where it is grown for both human consumption and animal feed. Given its reliability and productivity, cassava occupies a uniquely important position as a food-security crop for smallholder farmers in tropical areas where climate, soils or societal stresses constrain production. Its roots accumulate starch in the parenchyma, forming swollen storage organs, which are harvested after 8-24 months.

We consider that for a crop-improvement program to develop cultivars resistant to arthropod pests, at least five criteria must be met (Ortman and Peters, 1980):

- A germplasm bank (Plucknett *et al*., 1987) that is representative of the crop species and that contains ample genetic diversity

- Methodologies for mass rearing the pest
- Methodologies for distinguishing resistant and susceptible cultivars in the field or greenhouse
- Ample natural field populations of the pest to permit sufficient selection pressure
- A breeding scheme to incorporate heritable resistance into cultivars

In the case of cassava and the whitefly-resistance program, all five criteria were met.

3.1.1 *Germplasm bank*

The CIAT cassava germplasm bank contains nearly 6000 accessions, of which 93% are landraces (locally selected cultivars), collected from tropical and subtropical regions of the world, but mainly from the Neotropics. The remaining 7% of the germplasm collection are hybrids from specific crosses. Most accessions are traditional cultivars that represent centuries of cassava cultivation in diverse habitats, selected by farmers over a long period in the presence of an ample diversity of herbivore arthropods. This material offers entomologists and breeders a potential pool of pest-resistance genes.

The cassava germplasm bank is maintained in vitro (Withers, 1989). In addition, from 4000-4500 accessions are continually grown in the field, exposed to herbivore populations and available for continual screening for whitefly and other pest or disease damage.

3.1.2 *Methodologies for mass rearing the pest*

Methodologies have been developed for mass rearing *A. socialis* in the greenhouse, and about 20,000 whitefly adults can be produced daily (CIAT, 1995). Colonies are maintained on the susceptible cultivar CMC 40. Potted cassava plants containing high populations of *A. socialis* pupae and emerging adults are maintained in a fine-mesh screened chamber (6 m L x 3 m W x 3 m H) in the greenhouse (28-29°C and 70-75% RH). Twice a week, 30 (total 60), five-week-old potted cassava plants are exposed to whitefly adults by placing them in the infestation chamber.

Adults are allowed to oviposit for 72 h, after which they are removed from the plants. The plants are then removed from the chamber and placed in a separate greenhouse unit, where the immatures are allowed to develop. When whiteflies reach the pupal stage, the plants are returned to the chamber in order to harvest adults daily for use in resistance-mechanisms experiments, greenhouse screening or for supplementing field populations for germplasm evaluations. Immatures are used to maintain whitefly parasitoid colonies or to evaluate parasitoid efficacy.

3.1.3 *Methodologies for distinguishing resistant and susceptible cultivars in the field or greenhouse*

Field screening of cassava germplasm for resistance to whiteflies is done at several sites in Colombia where natural whitefly populations are high and damage levels are significant so as to distinguish susceptible cultivars. Whitefly adult and nymph feeding damage is most noticeable on the young, tender apical leaves of the cassava plant. Feeding induces a yellow-to-green mottled appearance and twisted or curled leaves, eventually resulting in chlorosis and defoliation. Field evaluations of cassava germplasm use a population (nymph and pupae) scale combined with a leaf-damage scale (Table 4). Evaluations are done periodically throughout the growing cycle. From 4-5 evaluations are done, 1 ½ to 2 months apart.

3.1.4 *Ample natural field populations of the pest to permit sufficient selection pressure*

Resistance screening using natural *A. socialis* populations is done primarily at two field sites in Colombia:

- Nataima, Tolima, in cooperation with CORPOICA, the Colombian Agricultural Research Corporation. *A. socialis* populations at this site have consistently been at moderate to high levels for nearly 15 years, offering an opportunity for sustainable research over a long period.
- CIAT headquarters, Palmira, Valle del Cauca. Initially, *A. socialis* populations at CIAT were low: Since 1994, however, populations have increased dramatically and are presently higher than in Tolima.

The purpose of the initial screening of accessions selected from the germplasm bank is to identify and discard susceptible genotypes. From 3 to 6 stem cuttings of each cultivar are planted in 2 replicates. Periodic evaluations, which begin about two months after germination, record leaf damage and populations of immature whiteflies. Nymphs are usually observed on the mid-to-upper leaves, and pupae are found on the mid-to-lower leaves of the plant. *A. socialis* pupae, which are black, surrounded by a white waxy secretion, are readily detected on the leaf undersurface. This methodology makes it possible to compare plant (leaf) damage and corresponding whitefly populations.

The presence of high whitefly populations does not ensure uniform infestation in a cassava field. Pockets of low populations and, therefore, low-selection pressure are often observed. Consequently some accessions showing little or no damage, or low populations may actually be "escapes." A common susceptible cultivar (usually CMC 40) is planted strategically throughout a screening block to measure the whitefly population levels, distribution and damage.

Those accessions selected as "promising" for resistance (i.e. low damage ratings and low whitefly populations) are reevaluated in subsequent cycles. It is common for an accession to be evaluated 6-7 times before it is considered resistant. As cassava has approximately one growing cycle per year, this is a long-term process, requiring a continued commitment in order to develop a whitefly-resistant hybrid. Promising clones that consistently received low damage ratings will enter into single-row yield trials (with and without pesticide application) to measure the impact of whitefly damage on cassava yields. The yield depression caused by whitefly feeding is an additional indication of the levels of resistance present in a particular cultivar. The most advanced lines from these trials are planted in large blocks (36-49 plants).

Varietal resistance is further evaluated in the laboratory by studying the effect of resistance on whitefly biology and behavior. Selected resistant cultivars and susceptible controls are grown from stem cuttings in pots for five weeks and infested with whiteflies from the CIAT colony of *A. socialis*. Infestations are made by attaching small (2.5 cm in diam.) clip cages to cassava leaves, held in place with a rigid rod imbedded in the soil. Ten whitefly females are introduced into each cage and left to oviposit for 24 h, after which the cages and adults are removed. The whitefly-infested plants are maintained in a growth chamber, where temperature (average 27°C), humidity (68± % RH), and photoperiod (12:12 h day/night) are regulated (Arias, 1995).

To determine the biological cycle of *A. socialis* on resistant and susceptible cultivars, from 50-200 eggs are selected per plant, and an "infestation map" was designed so that daily evaluations of eggs, nymphal instars and pupae development can be recorded. Each immature is evaluated with the aid of a stereomicroscope on the leaf undersurface. The potted plants, fastened to an iron support rod that allows upward-downward movement for optimal positioning, are inverted for easy observance. A rubber disk inserted at the base of the plant stem at the soil line prevents soil loss or plant movement and injury when the potted plant is inverted.

3.1.5 *Breeding scheme to incorporate heritable resistance into cultivars*

The crossing of whitefly-resistant parental genotypes with genotypes with high agronomic value is done in close collaboration with the cassava plant breeders. A process of selection and crosses and further selection will hopefully result in a cultivar combining resistance and high agronomic value. Because cassava is vegetatively propagated, the process need not go beyond the F_1 if a suitable hybrid is obtained. Once a superior type is obtained, it can be multiplied indefinitely (Bellotti and Kawano, 1980). Cassava farmers are brought into the process at an early stage, especially to determine whether the agronomic aspects (e.g. yield, ease of harvest, plant architecture, dry matter content, cooking, eating or processing quality) are adequate. The current breeding scheme being used to incorporate whitefly resistance into cassava hybrids at CIAT is described in Figure 1. If neither the level of resistance nor the agronomic properties are adequate in the F_1's, then the progeny can be crossed again to resistant or agronomically desirable genotypes and go through further selection.

3.2 Results

HPR studies initiated at CIAT more than 15 years ago have systematically been evaluating the nearly 6000 accessions in the CIAT cassava germplasm bank for resistance to whiteflies, especially *A. socialis*. More than 5000 accessions have now been evaluated at least once, primarily at two field sites in Colombia (CIAT HQ, Palmira and Tolima), using natural *A. socialis* populations. The number of clones evaluated now totals nearly 10,000. Those clones selected as promising for resistance may be evaluated several times. This accounts for the actual number screened being considerably higher than the number of accessions in the germplasm bank.

From 1992-2000, 5363 clones (several evaluated more than once) were evaluated in the field at the aforementioned sites (Fig. 2). Of these, 3897 (73%) were considered susceptible with damage ratings above 3.5 (see Table 4). The remaining 1466 genotypes (27%), with damage ratings below 3.5, were considered "promising" and will be reevaluated. Emphasis will be placed on those clones with damage ratings below 2.0 (8.9%). Most of these are probably escapes, where the selection pressure was not high enough.

Sources of resistance to *A. socialis* have now been identified. Clone M Ecu 72 has consistently expressed the highest level of resistance. Additional cultivars expressing moderate-to-high levels of resistance include M Ecu 64, M Per 335, M Per 415, M Per 317, M Per 216, M Per 265, M Per 266 and M Per 365. Based on these results, *A. socialis* resistance appears to be concentrated in germplasm originating from Ecuador and Peru; but this trend needs to be investigated further.

M Ecu 72 and M Bra 12 (an agronomically desirable clone with field tolerance to whiteflies) were used in a crossing program to provide high-yielding, whitefly-resistant clones. Thus far, 127 progeny have been produced from this cross and subsequently evaluated for whitefly resistance, yield and cooking-eating quality. After a series of field trials, primarily at the CORPOICA station in Tolima, four progeny (GC 489-34, CG 489-4, CG 489-31 and CG 489-23) meeting the above criteria were selected. These progeny have consistently displayed moderate levels of whitefly resistance, good yield and consumer quality. In field trials at Tolima, three showed no significant difference in yield between insecticide-treated and nontreated plots (insecticide applied on a monthly basis for 11 months to obtain infested and non-infested plants). The susceptible controls CMC 40 and H305-122 resulted in 52 and 79% yield reduction, respectively. Yields of the farmers' cultivar "Quindio" were reduced by 31%. Yield depression (between treated and nontreated plots) for CG 489-34, CG 489-23 and CG 489-31 was 3, 9 and 10%, respectively.

Resistance levels and mechanisms of the four hybrids and the two parents (M Ecu 72, female and M Bra 12, male) were evaluated in the laboratory and greenhouse. *A. socialis* biology and behavior were compared to susceptible CMC 40 and tolerant-resistant M Col 1505, using the previously described methodology (see Arias, 1995). These studies showed that *A. socialis* feeding on resistant clones had less oviposition, longer developmental periods, reduced size and higher mortality than those feeding on susceptible ones. *A. socialis* nymphal instars feeding on M Ecu 72 suffered 72.5% mortality, mostly in the early instars (Fig. 3). The resistant progenies CG 489-23, CG 489-4, CG 489-31 and CG 489-34 suffered mortalities of 50, 44, 42.5 and 34.5%, respectively, and the tolerant check M Col 1505 had a mortality of 45.0%. The susceptible check CMC 40 (33%) along with M Bra 12 (25.0%) had the lowest mortality. Although M Bra 12 shows some field resistance to whiteflies (and mites), it acted more like the susceptible controls in these evaluations. With respect to nymphal mortality, the hybrids (progeny) were intermediate between the resistant (M Ecu 72) and tolerant (M Bra 12) parents.

Although mortality is highest during the nymphal stages, mortality can also occur during the pupal stages. Preliminary evaluations with M Ecu 64 resulted in 71% mortality, 39.3% in the first instar and 16% in the pupal stage (data not shown). On highly resistant cultivars such as M Ecu 72, M Ecu 64 and M Per 415, first instar nymphs have difficulty in "attaching" themselves to the leaf undersurface to initiate feeding. These nymphs quickly desiccate and fall from the leaf surface.

The developmental period was longest on M Ecu 72 and the resistant hybrids and shortest on the CMC 40, M Col 1505 and M Bra 12 (Table 5). It is hypothesized that the longer developmental period may be used as an indicator of host resistance (Norris and Kogan, 1980). However the differences in average duration (days) between resistant and susceptible hybrids, although significant, were not large. For instance, the difference between M Ecu 72 and CMC 40 was only 2.4 days or approximately 7% (Table 5).

Nymphal size was compared on M Ecu 72 (R) and CMC 40 (S). Nymphs developing on CMC 40 were significantly larger than those developing on the resistant cultivar M Ecu 72 (Table 6). These differences are especially noticeable in the length of the second and third instar nymphs and pupae. A comparison of pupal size on eight clones resulted in significant varietal differences (Table 7). M Ecu 72, CG 489-4, CG 489-34 and CG 489-31 had a smaller pupal size than the other clones. These results indicate a probable antibiosis mechanism in the resistant clones.

Ovipositional preference was measured in the field at CIAT during the dry season when *A. socialis* populations were high. One potted plant of each of the eight cultivars was placed in a field cage and inoculated with four different whitefly densities (1714, 1286, 857 and 429 adults per cage) and replicated five times. After a 24-hour exposure, oviposition was highest on M Col 1505 (average of 384 eggs for the four adult densities) and CMC 40 (355 eggs/clone) and lowest on M Ecu 72, CG 489-31 and CG 489-34 with 107, 67 and 70 eggs per clone, respectively (Table 8).

4.0 Conclusions and Future Research

This paper presents a representative review of research activities in HPR to whiteflies, with emphasis on *A. socialis* resistance in cassava. It is not meant to be a comprehensive review, undoubtedly there is more research going on in this area than we described herein. Nevertheless, there are some general observations that can be made:

- Whitefly HPR research has increased in recent years, primarily on the *B. tabaci* complex.
- A narrow range of germplasm has been tested, and there are very few deliberate breeding programs aimed at developing higher levels of resistance in cultivars.
- There is a limited number of related wild species being evaluated or used as a source of whitefly resistance for breeding programs.
- There is limited research being done to combine resistance to crop viruses and whiteflies in the same genotype.

Special emphasis has been placed on our ongoing efforts to develop whitefly-resistant cultivars in cassava. We feel that this project is unique in that we are systematically screening a large germplasm bank (≈ 6000 clones). We are identifying resistant genotypes and through a comprehensive breeding scheme, developing commercial hybrids containing whitefly resistance.

Several whitefly-resistant hybrids have been developed, and three of them (CG 489-31, CG 489-34 and CG 489-23) are being evaluated by CORPOICA as part of a process prior to official varietal release. Hybrid CG 489-31 is performing best in field trials, resulting in high yields, commercially acceptable cooking and eating quality, and good *A. socialis* resistance. It is expected that the hybrid will be released during 2001. Cassava germplasm evaluations will continue to identify sources of whitefly resistance in the landrace cultivars in the CIAT germplasm bank, and these will enter into the breeding scheme.

Resistance to *B. tabaci* biotype (B), which feeds on cassava, is now being evaluated. This research has been initiated at CIAT, and a colony of *B. tabaci* has now been established on cassava. Plans are also being developed to evaluate this resistant germplasm with the *B. tabaci* biotype feeding on cassava in Africa. In Africa *B. tabaci* is the vector of ACMD, the cause of considerable crop loss on that continent (Thresh *et al*., 1994). Efforts are therefore under way to combine the resistance to the viral disease (there are good levels of resistance to ACMD) with that of the whitefly in cassava. Crosses between ACMD- and whitefly-resistant genotypes are being made at CIAT, and these can eventually be evaluated in Africa for resistance to ACMD and *B. tabaci*.

Research is presently under way at CIAT to identify the genomic regions responsible for whitefly resistance in cassava. It is expected that this research, funded by MFAT (The Ministry of Foreign Affairs) of New Zealand, will lead to the identification of molecular makers linked to the whitefly resistance gene(s) and provide the tools for the possible cloning of these genes.

A mapping population (a population of genotypes suitable for identifying molecular markers for a given trait) using M Ecu 72 as the resistant parent and M Col 2246 as the susceptible parent was developed. Initially, we found a high level of polymorphism (>60%) between these two parents using a set of genomic microsatellites. We are also screening the population from this cross (282 individuals) with a new set of microsatellites generated at the CIAT lab from cDNA libraries and with Amplified Fragment Length Polymorphism (AFLP) markers. Segregation data from the microsatellites, AFLP markers and greenhouse evaluations of the 282 F1 individuals will be used for constructing a linkage map and for Quantitative Trait Loci analysis of whitefly resistance. Molecular genetic markers closely linked to the resistance gene(s) would allow a more efficient identification of resistant materials in breeding programs and improve the efficiency of cassava breeding. This work also has broader implications given that the identification of such markers is a necessary first step to fine-mapping and cloning the resistance gene(s) that will provide a better understanding of the type of resistance to whiteflies.

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Table 1. Studies evaluating the *B. tabaci* species complex: Oviposition/feeding on different crop species.

Crops Compared	Observations	References
Cotton, broccoli, cantaloupes, lettuce	Highest egg/population on cantaloupes, followed by cotton; broccoli least preferred	Chu *et al*., 1995
Zucchini, cantaloupes, cotton, Pumpkins, lettuce, tomatoes	Zucchini highest whitefly survival; tomatoes lowest	Costa *et al*., 1991
Soybeans vs. groundnuts	Fewer eggs laid on groundnuts in field, trap-crop experiments	McAuslane *et al*., 1995a
Cotton vs. poinsettias	No significant differences in whitefly development time & longevity	Bethke *et al*., 1991
Brassica oleraceae	Cabbage & broccoli less infested than kale, collards & brussel sprouts	Elsey & Farnham, 1994
Squash vs. zucchini	Squash supported larger whitefly populations	McAuslane *et al*., 1996
Zucchini, cabbage, sugar beets	Zucchini preferred over other hosts	Blua *et al*., 1995

Table 2. Examples of HPR screening or evaluations of crop germplasm for resistance to *B. tabaci* species complex.

Crop	Country	Genotypes		Reference
		Evaluated[1]	Selected	
Alfalfa	USA	73 plants from 10,000 1/2sib (F)	2 families with resistance	Teuber *et al*., 1996
Brassica oleraceae	USA	64 (F, C)	Glossy leaves associated with resistance	Farnham & Elsey, 1995
Common beans	Puerto Rico	41 (F)	?	Blair & Beaver, 1993
Common beans	Puerto Rico	4 (G)	2 genotypes less preferred	Peña Rojas *et al*., 1992
Cotton	Turkey	19 (F)	3	Ozgur & Sekeroglu, 1986
Cotton	Israel	3 (F)	1 (glabrous)	Navon *et al*., 1991
Cotton & wild relatives	USA	19 (F)	1 (wild species)	Wilson *et al*., 1993
Gossypium spp.	USA	24 (F, G)	4 genotypes low eggs/nymphs	Meagher *et al*., 1997
Groundnuts	USA	150 (F)	0 (no resistance)	McAuslane *et al*., 1995b
Melons	USA	31 (G)	8 (less damage)	Simmons & McCreight, 1996
Melons	Venezuela	8 (F)	2	Morales & Bastidas, 1997
Soybeans	USA	14 (F)	3	Lambert *et al*., 1997
Soybeans	USA	36 (F)	7	McPherson, 1996
Summer squash	USA	19 (F)	Differences in susceptibility	Paris *et al*., 1993
Tomatoes	India	1200 (F)	3	Channarayappa *et al*., 1992
Tomatoes-commercial	USA	20 (L)	(ovipositional differences)	Heinz & Zalom, 1995
Wild tomatoes	USA	7 (L)	2	Heinz & Zalom, 1995

[1] (F) = field, (G) = greenhouse, (L) = laboratory, (C) = cages

Table 3. Crops with genotypes reported showing some resistance to the *B. tabaci* species complex.

Crop	Resistance		Reference
	County	Mechanism/Factor	
Zucchini	USA	Tolerance	Cardoza *et al*., 1999
Melons	Venezuela	Antixenosis	Morales & Bastidas, 1997
Soybeans	USA	Antixenosis	Lambert *et al*., 1995
Tomatoes	India	Antixenosis (thrichomes)	Channarayappa *et al*., 1992
Tomatoes	USA	Trichome density	Heinz & Zalom, 1995
Lettuce	USA	Latex (entrapment)	Dussourd, 1995
Tomatoes (wild)	USA	Acylsugars	Liedl *et al*., 1995
Cotton	USA	Not indicated	Smith *et al*., 1998
Cotton	Spain	Tolerance (varietal release)	Gutierrez, 1997
Soybeans	USA	Glabrousness	McAuslane, 1996
Broccoli	USA	Glossy foliage	Farnham & Elsey, 1995
Melons	USA	Glabrousness	Riley *et al*. 2001

Table 4. Population and damage scales for evaluating cassava germplasm for resistance to whiteflies.

Population scale (nymphs & pupae)
1 = no whitefly stages present
2 = 1-200 individuals per cassava leaf
3 = 201-500 per leaf
4 = 501-2000 per leaf
5 = 2001-4000 per leaf
6 = > 4000 per leaf
Damage scale
1 = no leaf damage
2 = young leaves still green but slightly flaccid
3 = some twisting of young leaves, slight leaf curling
4 = apical leaves curled & twisted; yellow-green mottled appearance
5 = same as 4, but with sooty mold & yellowing of leaves
6 = considerable leaf necrosis & defoliation, sooty mold on mid & lower leaves and young stems.

Table 5. Developmental time of *A. socialis* from egg to adult on eight cassava clones in a growth chamber (28ºC ± 1; RH 70% ± 10) (Arias, 1995).

Clone	N	Average Duration (Days)	Standard Deviation
M Ecu 72	55	34.5 A	1.8
CG 489-31	115	33.7 B	1.9
CG 489-4	112	33.2 B	1.9
CG 489-34	131	33.1 B	2.3
CG 489-23	100	33.1 B	1.8
M Bra 12	150	32.2 C	1.6
CMC-40	132	32.1 C	1.9
M Col 1505	110	31.9 C	2.0

Values with same letter are not significantly different (P=0.05, Ryan-Einot-Gabriel Welsch multiple F-test).

Table 6. Effect of two cassava clones[1], CMC 40 (susceptible) and M Ecu 72 (resistant) on average length and width of the whitefly *A. socialis*.

Stage	Average Length (mm)[2]						Average Width (mm)			
	No.	CMC 40	SD	No.	M Ecu 72	SD	CMC 40	SD	M Ecu 72	SD
Egg	29	0.08	0.00	31	0.08	0.01	0.03*	0.00	0.04	0.00
Nymph I	52	0.23	0.01	87	0.23	0.02	0.11*	0.01	0.12	0.01
Nymph II	55	0.32*	0.01	44	0.31	0.01	0.19	0.01	0.18	0.01
Nymph III	61	0.41*	0.04	68	0.34	0.04	0.26	0.03	0.25	0.03
Pupae	66	0.62*	0.05	86	0.58	0.05	0.36*	0.03	0.34	0.03

[1] Data represents the most susceptible resistant of eight tested cassava clones (Arias, 1995).

[2] Values with asterisks (*) are significantly different (P=0.05, Ryan-Einot-Gabriel Welsch multiple F-test).

Table 7. Average length and width of the pupal stage of the whitefly *A. socialis* after developing on eight different cassava clones (Arias, 1995).

Clone	No.	Avg. Length[1] (mm)	SD	Avg. Width[1] (mm)	SD
M Col 1505	80	0.63 A	0.05	0.36 AB	0.03
CMC 40	66	0.61 AB	0.05	0.36 A	0.03
CG 489-23	81	0.61 B	0.04	0.34 BCD	0.03
M Bra 12	85	0.61 B	0.05	0.35 BC	0.03
CG 489-4	53	0.60 BC	0.05	0.33 D	0.03
CG 489-34	60	0.59 C	0.05	0.34 CD	0.03
M Ecu 72	86	0.58 CD	0.05	0.34 CD	0.03
CG 489-31	59	0.57 D	0.03	0.32 E	0.02

[1] Values with same letter are not significantly different (P=0.05, Ryan-Einot-Gabriel Welsch multiple F-test).

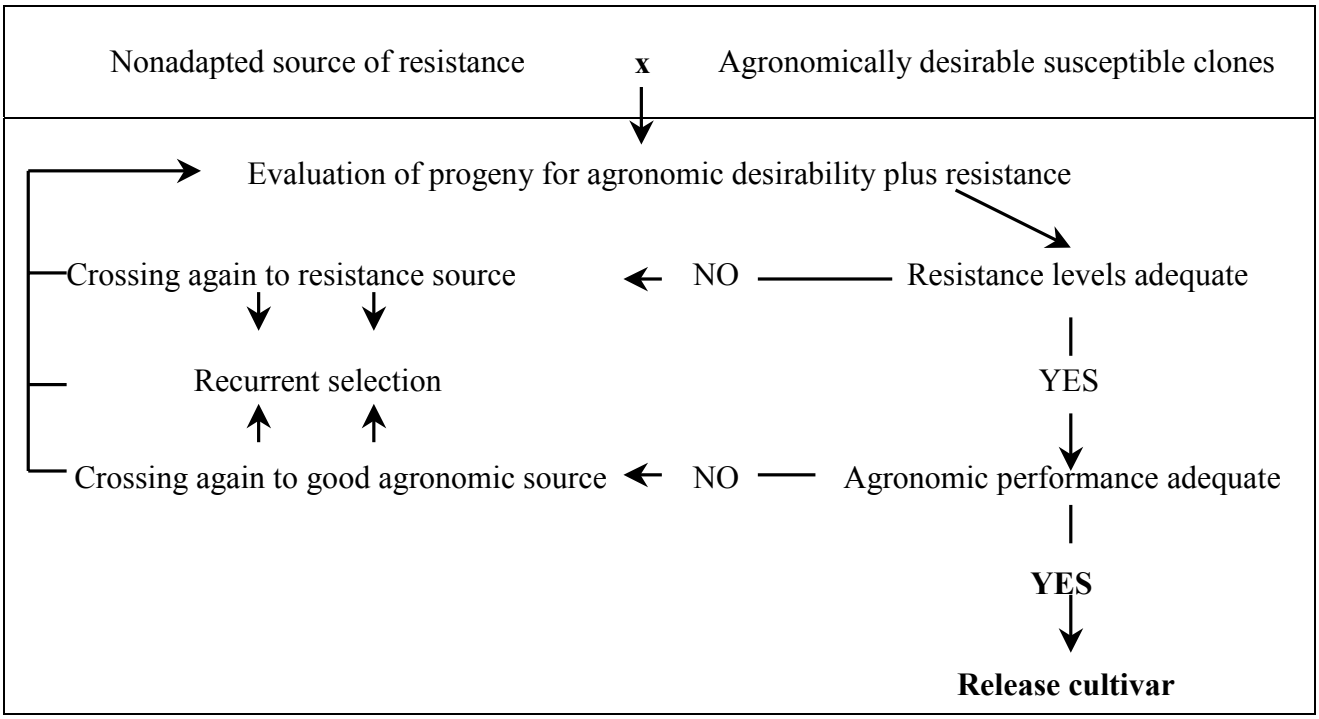
Table 8. Average oviposition of *A. socialis* on eight cassava clones in field cages during the dry season (Arias, 1995).

Clone	Avg. No. Eggs/Clone[1, 2]
M Col 1505	384.4 A
CMC 40	355.2 A
M Bra 12	237.6 AB
CG 489-23	117.9 BC
CG 489-4	122.8 BC
M Ecu 72	107.7 BC
CG 489-31	67.4 C
CG 489-34	70.4 C

[1] Average of four different whitefly inoculation densities; values with same letter are not significantly different (P=0.05, Ryan-Einot-Gabriel Welsch multiple F-test).

[2] Data was transformed using Log (eggs + 1) to reduce the impact of heteroscedasticity.

Figure 1. Scheme for incorporating whitefly resistance from nonadapted cassava sources into commercial hybrids.



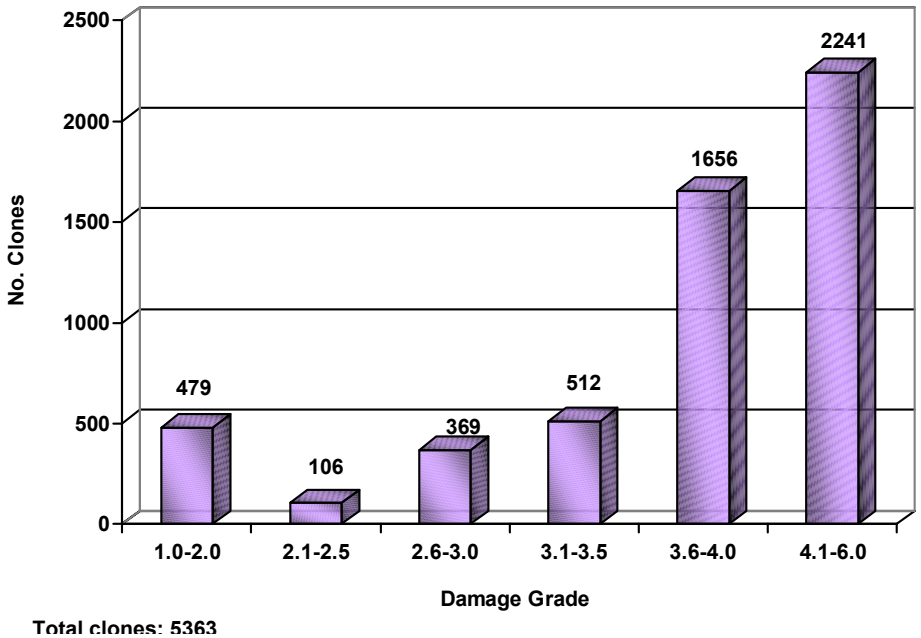


Figure 2. CIAT cassava germplasm evaluated in Colombia for resistance to whiteflies (*A. socialis*) from 1992 to 2000; damage scores are based on a 1 (no damage) to 6 (severe damage) rating scale.

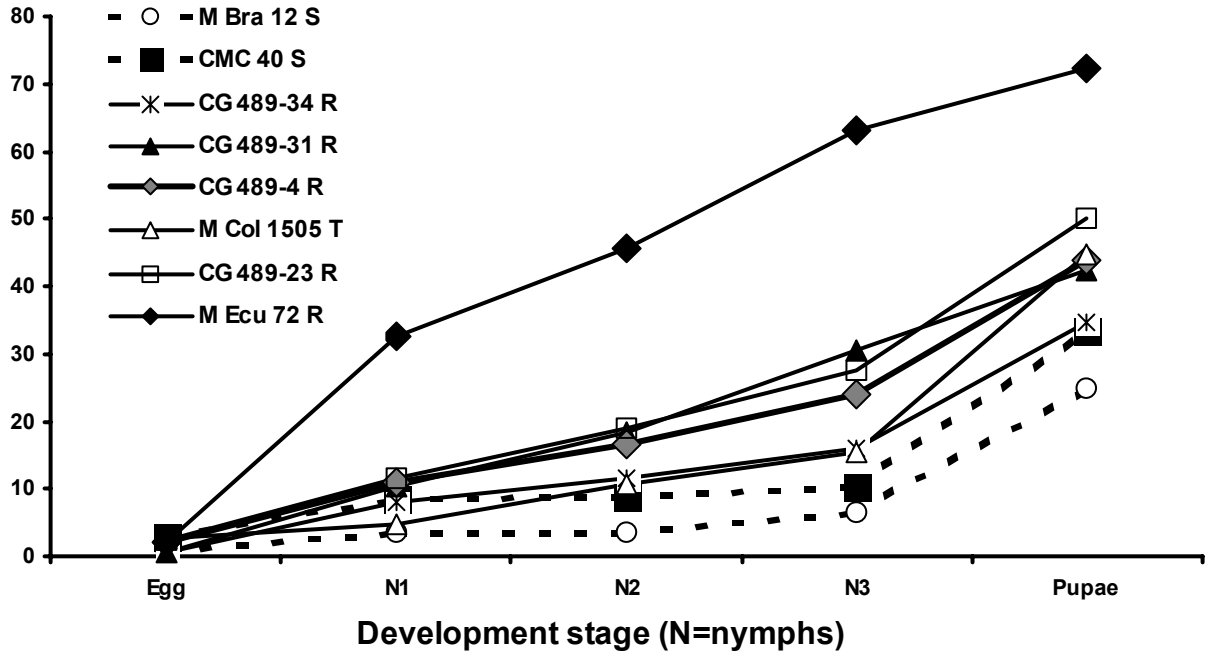


Figure 3. Whitefly (*Aleurotrachelus socialis*) nymphal mortality on resistant (R) tolerant (T) and susceptible (S) cassava clones.

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