CHAPTER 10

Insects and Mites that Attack Cassava, and their Control*

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Introduction

Cassava (*Manihot esculenta* Crantz) is a major energy source for millions of people who live in the tropics and subtropics. In the last 26 years, considerable efforts have been made to study the crop and its associated pest complex. Research entities include several international organizations such as the Centro Internacional de Agricultura Tropical (CIAT)[6] in Colombia, the International Institute of Tropical Agriculture (IITA) in Nigeria, and the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), in Costa Rica; and many national programs in Latin America (e.g., Colombia, Brazil, and Cuba), Africa (e.g., Cameroon, Nigeria, and Uganda), and Asia (e.g., India, Indonesia, China, and Thailand) (Bellotti et al. 1999; Bellotti 2000b).

Cassava, as plant and crop, originates in the Neotropics. However, the exact place of origin is debatable, but was probably within a wide region of the Amazon Basin, encompassing various habitats (Renvoize 1973; Allem 1994). Bellotti et al. (1994) suggest that this may be one reason why such a diversity of arthropods is recorded as attacking the crop in the Americas (Table 10-1). The host plant does, indeed, display broad genetic variation, which correlates with the numerous types of organisms that feed on the plant or are in symbiosis with it. Of the 17 general groups of pests described in Table 10-1, 35 species are found in America, 11 in Africa, and 6 in Asia. In all, about 200 arthropod species feed on cassava (Bellotti and Schoonhoven 1978a, 1978b). Many are specific to cassava, having adapted, in diverse ways, to this species' natural biochemical defenses, which include laticifers and cyanogenic components (Bellotti and Riis 1994; Bellotti 2000a).

Many of these species are minor pests and cause few or no losses in yield. Others are classified as major pests because, apparently, they have co-evolved with the crop, which has then become their principal or only host. These pests can cause severe damage to the crop, as manifested in yield losses. Such major pests include mites, whiteflies, thrips, mealybugs, lace bugs, stemborers, hornworm, and subterranean burrower bug. Other pests such as insect scales, leafhoppers, white grubs, cutworms, leafcutting ants, fruit flies, shoot flies, and termites can cause sporadic or local damage to the crop. These are considered as minor or generalist pests, and may attack the crop opportunistically, especially during drought when the only source of available food is cassava (Bellotti 2000b).

Insects harm cassava by reducing the photosynthetically active area of the plant (leaves), thus diminishing yields; attacking stems, which debilitates the plant's support and inhibits transport of nutrients; and attacking planting materials ("seed") and thus reducing shoot production in stake germination. They can also attack roots and cause secondary rots. Some pests are vectors and spread diseases.

Observations indicate that pests attacking the plant over a prolonged period—such as mites, whiteflies,

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Table 10-1. Global distribution of arthropod pests important to the cassava crop.

Pest	Principal species	Americas	Africa	Asia
Mites	*Mononychellus tanajoa*	X	X	
	Tetranychus urticae	X		X
	Oligonychus peruvianus	X		
Mealybugs	*Phenacoccus manihoti*	X	X	
	P. herreni	X		
Root mealybugs	*Pseudococcus mandioca*	X		
	Stictococcus vayssierei		X	
Whiteflies	*Aleurotrachelus socialis*	X		
	Aleurothrixus aepim	X		
	Bemisia tabaci	X	X	X
	B. tuberculata	X		
Hornworms	*Erinnyis ello*	X		
	E. alope	X		
Lace bugs	*Vatiga illudens*	X		
	V. manihotae	X		
	Amblystira machalana	X		
Burrower bug	*Cyrtomenus bergi*	X		
Thrips	*Frankliniella williamsi*	X	X	
	Scirtothrips manihoti	X		
	Corynothrips stenopterus	X		
Scale insect	*Aonidomytilus albus*	X	X	X
Fruit flies	*Anastrepha pickeli*	X		
	A. manihoti	X		
Shoot flies	*Neosilba perezi*	X		
	Silba pendula	X		
Gall fly	*Jatrophobia (Eudiplosis) brasiliensis*	X		
White grubs	*Leucopholis rorida*	X	X	X
	Phyllophaga spp.	X		
	Others	X		
Termites	*Coptotermes* spp.	X	X	X
	Heterotermes tenuis	X		
Stemborers	*Chilomima* spp.	X		
	Coelosternus spp.	X		
	Lagocheirus spp.	X	X	X
Leafcutting ants	*Atta* spp.	X		
	Acromyrmex spp.	X		
Grasshoppers	*Zonocerus elegans*		X	
	Z. variegatus		X	
Total		**35**	**11**	**6**

SOURCE: Bellotti 2000b; Arias and Bellotti 2001.

thrips, mealybugs, stemborers, ins ect scales, and lace bugs—will reduce yield more extensively than those that cause defoliation and damage to plant parts over short periods. Some pests, such as the hornworm, leafcutting ants, fruit flies, and shoot flies, allow the cassava plant to recover from short-term damage, particularly if this is not repeated.

Because cassava is a crop that is mostly grown in marginal areas, it usually faces prolonged dry seasons and deficient soils (abiotic factors) and many pests and diseases (biotic factors). Farmers in such areas are often in a difficult socioeconomic situation. When a cassava planting is planned, selecting varieties that are resistant or tolerant of most these biotic factors is therefore important. This way, farmers do not need to resort to the application of pesticides in the crop's first months. Nor do they need to accept losses of root yield because of pests and diseases. Varietal resistance, or host-plant resistance (HPR), thus becomes a significant pest control measure. Other control measures such as appropriate farming practices, pesticide applications, and biological control are also used, and are discussed in more detail below.

Cassava Arthropod Pest Complex

Cassava is a no vegetation production cycle develops over 1 to 2 years—a long cycle for a commercial crop. It propagates vegetatively and has considerable drought tolerance. It is usually planted with other species, either as an intercrop or in staggered rotation, the system most commonly used by farmers. Such agronomic characteristics contribute, without doubt, to the diversity of the arthropod pests feeding on this crop.

The arthropod pest complex extends over a broad region of the crop's production area, highlighting the need for care in placing quarantine measures to prevent pathogens being introduced into pest-free areas (Frison and Feliu 1991). The accidental introductions of the cassava green mite (*Mononychellus tanajoa* Bondar or CGM) and mealybug (*Phenacoccus manihoti* Mat. Ferr.) from the Americas into Africa have caused considerable losses throughout the African cassava belt and have required a massive effort in biological control (Herren and Neuenschwander 1991; Neuenschwander 1994a). In Asia, none of the principal cassava pests has yet been established and the arthropod pests so far observed have not caused serious losses in yield (Maddison 1979).

Recent explorations in the Neotropical cassava-growing areas indicate that the arthropod pest complex is not geographically uniform. For example, the mealybug *Phenacoccus herreni*, which causes considerable damage in Northeast Brazil, was probably introduced from northern South America (Venezuela or Colombia), where this insect's populations are controlled by natural enemies not found in Brazil (Bellotti et al. 1994; Smith and Bellotti 1996). *Phenacoccus manihoti*, a serious pest in Africa, is found only in Paraguay and certain areas of the State of Mato Grosso in Brazil and of the Department of Santa Cruz in Bolivia (Lohr and Varela 1990; Bellotti 2000a, 2000b). Studies on the CGM have demonstrated a high degree of polymorphism and a large complex of *Mononychellus* species in northern South America, unlike what is found in Brazil (Bellotti et al. 1994). This diversity is associated with the great wealth of phytoseiids that control *Mononychellus* spp. in cassava crops (Bellotti et al. 1987, 1999; Bellotti 2000a).

Insects that Attack Planting Materials

The planting of stakes free of insect pests and other damage is important for obtaining good shoot development (i.e., germination) and the satisfactory establishment of young plants.

Insect scales

Various species of insect scales have been identified as attacking cassava stems in many cassava-producing regions of the world. The quality of planting materials can be noticeably reduced if stakes are infested with scales.

- White scale, *Aonidomytilus albus* (Cockerell), can reduce shoot development by 50% to 60%, according to the severity of infestation. Immersing infested stakes in insecticide solutions reduces infestations but heavily infested stakes will germinate poorly even after treatment. Accordingly, stakes infested with scales are not recommended for use as planting materials. *Aonidomytilus albus* has been found in most cassava-producing regions of the world.

- Individuals of black scale or *Saissetia miranda* (Cockerell & Parrott), gray scale or *Hemiberlesia diffinis* (Newstead), and *Ceroplastes* sp., as well as those of *A. albus*, are not noticeable when populations are low or are found in young crops. Instead, they are highly visible in older crops, where isolated plants or sections of the crop become heavily infested and from which epizootics can start in a following cropping cycle if stakes are not selected and treated. Burning of harvest residues is advisable for preventing these pests from resurging.

Fruit fly

Two species of fruit fly have been identified as attacking cassava in the Americas: *Anastrepha manihoti* da Costa Lima and *A. pickeli* da Costa Lima. The larvae of this fly tunnels up or down the plant's stems, forming brown galleries in the pith, thereby promoting stem rot.

In mature plants, affected stems have light to dark brown pith, with an aqueous appearance due to the association existing between this pest and a bacterium, *Erwinia carotovora*. Germination of stakes obtained from such plants may be reduced by as much as 16%, taking several weeks. This pest is described below in more detail under the section "Stem-perforating insects", page 235.

Stemborers

Stemborers, mostly belonging to the orders Lepidoptera and Coleoptera, have been found in stakes used for planting. Infestation usually occurs when plants are growing and also during storage of planting materials. Stored stakes should be carefully inspected before use. Normally, these insects are detected by the presence of galleries and perforations in the stem, accompanied by such signs as milky exudates, fine or coarse sawdust, residues of protective tissues, stem parts, and cankers.

Insects that Attack Stakes and Seedlings

White grub

Together with the Spanish names *mojojoy* and *mojorro*, this name describes beetle larvae (Coleoptera) that attack cassava. They are white, measuring about 5 cm. Their dark coffee-colored heads carry large jaws. Three pairs of legs are found in the thoracic area, and the abdomen is prominent and dark.

They are easy to find, as they live in the top 15 to 30 cm of the soil or on its surface in decomposing organic matter (e.g., trunks and leaves), adopting a crescent or "C" position. However, when temperatures are high and humidity drops, they tend to burrow deep into the soil, seeking cooler and damper places. This makes their control more difficult. They feed on plant roots, that is, they are rhizophagous, and tend to damage newly planted stakes, either before or after shooting (or germination) (FIDAR 1998).

A worldwide pest. White grubs are a cassava pest throughout the world and constitute a serious problem in Indonesia, where the most important species appears to be *Leucopholis rorida*. Another significant pest comprises the *Phyllophaga* spp. in Colombia. The literature also mentions the following: *Lepidiota stigma, Euchlora viridis, E. nigra, E. pulchripes, Anomala obsoleta, Heteronychus plebejus, Opatrum micans, Carpophilus marginallus, Dactylosternum* sp.*, Inesida leprosa, Petrognatha gigas*, and *Sternotomis virescens* (Leefmans 1915; Dulong 1971; CIAT 1976).

The white grubs most frequently found in Colombia belong to the family Melolonthidae, which has four subfamilies: Cetoniinae, Melolonthinae, Dynastinae, and Rutelinae. Victoria and Pardo (1999) found that the principal genera of rhizophagous white grubs that attack cassava in the Department of Cauca are *Phyllophaga* sp. (Melolonthinae), *Cyclocephala* sp. (Dynastinae), and *Anomala* sp. (Rutelinae). However, the study of subterranean pests in Colombia verified that white grubs form a complex by virtue of abundance of species, lack of crop specificity, and their temporary and local action.

Victoria and Pardo (1999) used black light traps in several sites in the Municipalities of Caldono, Buenos Aires, and Santander de Quilichao (Department of Cauca) and collected 21,739 examples belonging to 44 species of the subfamilies Dynastinae, Rutelinae, and Melolonthidae. Most had been already recorded for their economic importance to the region and other parts of the country. Captured specimens belonged to the genera *Aspidolea*, *Cyclocephala*, *Stenocrates*, *Ancognatha*, *Dyscinetus*, *Coelosis*, *Strategus*, *Podischnus*, *Golofa*, *Ligyrus*, *Phileurus*, *Plectris*, *Phyllophaga*, *Astaena*, *Chariodemia*, *Macrodactylus*, *Isonychus*, *Barybus*, *Pelidnota*, *Anomala,* and *Leucotureus*.

The damage that these grubs cause consists of destroying the cortex of planted stakes, so that their tissues rot and die. When 1 to 3-month-old plants are attacked, leaves wilt and the plants suddenly die because the larvae feed on the cortex at the base of the stem. They usually feed under the soil, forming tunnels within the stake, preventing nutrients from moving towards the plant's aerial parts. Furthermore, they consume newly forming roots.

Biology. The biology of *Leucopholis rorida* in Indonesia is described as follows, with respect to the cassava crop. Adults are active at the beginning of the rains, but the most severe damage occurs 4 to 6 months later. Nine days after mating, females oviposit deeply in the soil, at 50 to 60 cm. They lay up to 37 pearly white individual eggs that hatch within 3 weeks. The larval stage lasts for almost 10 months, with the 4 to 6-month-old larvae being the most destructive. The larvae live at depths of 20 to 30 cm, where they feed on roots of cassava and other hosts, including maize, rice, grasses, and sweet potato. Pupae are found more deeply, at about 50 cm. The prepupal stage lasts for 14 days and the pupal, about 22 days.

The grubs undergo complete metamorphosis: egg, larva (grub), prepupa, and pupa. The larval or grub stage undergoes three instars, with their capacity to eat increasing as they develop, doing the most damage during the third instar.

The larval stage lasts from 3 or 4 months to 9 months, according to species. Genera of shorter larval stages that attack cassava include *Anomala* and *Cyclocephala*. These have short biological cycles, having two generations a year that appear in the two rainy periods, that is, March–April and October–November. This type of grub is known as *bivoltine*. Other genera have longer biological cycles, appearing once a year, that is, they are *univoltine*. This second group includes the *Phyllophaga* spp., the economically most important genus of cassava pests in Colombia.

Attacks occur most frequently when cassava grows in a soil previously occupied by grasses or weeds. At soil preparation, high populations of larvae are usually seen.

Biological control. Several parasitoids, predators, and entomopathogens have been identified as attacking white grubs. The most studied of these are the entomopathogens, including the fungi *Metarhizium anisopliae* and *Beauveria bassiana*, and the bacterium *Bacillus popilliae*, which causes milky disease of white grubs. Experiments carried out at CIAT (1974) indicated that the fungi can effectively control the grubs.

Londoño (1999) indicated that some natural enemies of white grubs are found in eastern Antioquia. Not only are they useful for their natural incidence but also because they cause significant mortality when inoculated into the soil. These enemies include the three organisms mentioned above (*M. anisopliae, B. bassiana*, and *Bac. popilliae*) and *Beauveria brongniartii*, which, under controlled conditions, cause 50% mortality.

Londoño (1999) had good results when he used insectariums to evaluate 36 isolates of organisms for their control of white grubs. Among the control agents were nematodes *Steinernema carpocapsae*, which caused 90% mortality, and *Heterorhabditis* sp., which achieved 70%. According to Londoño and De Los Ríos (1997), these organisms could cause mortality as high as 100%.

Victoria and Pardo (1999) searched for natural enemies in several sites in the Department of Cauca and found the following entomopathogens associated with white grubs: *M. anisopliae* in seven sites, *B. bassiana* in one site, *Bac. popilliae* in two sites, and several nematodes in seven sites.

Parasitoids and predatory insects are not well studied, but the following have been found: dipterans of the families Tachinidae (10 sites) and Asilidae (one site), and an elaterid coleopteran (*Elateridae* pos. *Conoderus*) in four sites. Hymenopterans were found in two of 21 sites.

Chemical control. White grubs are effectively controlled by lorsban (30 to 40 kg of paste concentrate or p.c. per hectare) or carbofuran (3 to 4 g of p.c. per plant), applied under the stakes in the soil. Treatment by immersing stakes in insecticide solutions is not as effective as applications to moist soil. Another treatment also used when plants are small is liquid carbofuran 4F applied to the soil at the plants' base.

Cutworms

Several species of cutworms attack cassava, damaging the plants in three ways according to their location in the soil:

- *Ground cutworms*, for example, *Agrotis ipsilon*, damage seedlings near the soil surface (either on or under it), leaving the cut piece lying on the soil. These larvae are dark gray with a greasy aspect or brown with streaks of light colors.

- *Climbing cutworms*, for example, *Spodoptera eridania* and *S. sunia*, climb up the stems of seedlings and consume buds and leaves before finally making annular cuts in the stems, which cause plant wilt and death. The well-developed larva is dark gray or almost black, with yellow or orange lateral bands.

- *Subterranean cutworms* remain in the soil and feed on the roots and underground stem parts, causing losses in planting materials. Losses of young plants can reach 50%, making it necessary to replant.

The biology is similar for the three categories of cutworms that attack cassava. Eggs are oviposited en masse on the lower side of leaves close to the soil. They hatch in 6 to 8 days, and are fully developed within 20 to 30 days. The pupal stage (8 to 11 days) occurs in the soil or under plant residues. Oviposition starts about a week after adults emerge. One generation lasts almost 2 months and, under favorable environmental conditions, several generations may occur in 1 year.

Cutworm attacks are sporadic and usually occur in foci or patches in the crop. They occur more frequently when cassava follows maize or sorghum or when it is planted in lots adjacent to these crops. Longer stakes (30 cm) enable the plants to recover when under attack.

These insects can be effectively controlled with poisoned feed applied to the soil surface (10 kg of sawdust, 8–10 L of water, 500 g of sugar or 1 L of molasses, and 100 g of trichlorform per quarter or half hectare). They can also be controlled with applications of lorsban around the stakes.

Crickets

As soon as they emerge, crickets, *Gryllus assimilis* or common cricket and *Gryllotalpa* sp. or mole-cricket, cut young shoots. They also damage the plant's base, which then becomes more susceptible to lodging by wind. Crickets are controlled by using the same products as recommended for cutworms.

Termites

Termites—a tropical lowland pest—may attack cassava. They are reported as pests in various cassava-producing regions of the world, particularly Africa. In Madagascar, *Coptotermes voeltzkowi* and *C. paradoxus* of the family Rhinotermitidae feed on planting materials, roots that have bulked, and growing plants. The principal damage they cause appears to be stake loss, which seriously affects crop establishment, especially during prolonged dry periods. Bulked roots damaged by termites later rot.

In Colombia, *Heterotermes tenuis* and *Coptotermes niger* feed on planting materials (stakes), roots, or growing plants. Attacked parts then dry or die, particularly if climatic conditions are unfavorable, certain pathogens are present, or stakes are of poor quality. Stakes must be protected at crop establishment if shoot development is to be good and the plants are to "germinate" effectively. Protection may consist of combinations of treatments, such as an application of the fungicides captan + carbendazim (2 g of a.i./L water) with a later application of the insecticide lorsban in powder (3 to 4 g per site or stake) to the soil.

Leaf-Eating Insects

Cassava hornworm

Erinnyis ello (L.), family Sphingidae, is a major cassava pest in the Neotropics (Bellotti and Riis 1994; Bellotti et al. 1992, 1994, 1999). It has a broad geographical habitat, ranging from southeastern Brazil, Argentina, and Paraguay to the Caribbean Region and southeastern USA. The migratory capacity of *E. ello*, its broad climatic adaptation, and wide host range comprise the probable reasons for its extensive distribution and sporadic attacks (Janzen 1987).

Other *Erinnyis* species also feed on cassava, including the subspecies *E. ello encantado* and a closely related species, *E. alope*, which have been recorded in the Neotropics. The insect has not yet been reported in either Africa or Asia.

Biology and behavior. All hornworm larvae feed on young and mature cassava leaves and on tender stems and shoots. Severe attacks cause complete defoliation of the plant, loss in root volume, and poor root quality. Even though yield loss can be severe through complete defoliation after one or several attacks, the cassava plant itself does not die. The carbohydrates stored in the roots enable the plant to recover, especially during favorable conditions such as the tropical rainy season. Repeated attacks are very common when pesticides are not applied in time, as they do not destroy fifth-instar larvae or prepupae. Instead, the pesticides eliminate the pest's natural enemies (Braun et al. 1993). Large cassava plantings are prone to frequent and repetitive attacks from this pest.

Defoliation during the initial months of crop growth can cause significant yield losses. In simulation studies, losses have been estimated to be between 10% and 64%, according to the intensity of attack, number of attacks, and the ecosystem where the crop is developed (Arias and Bellotti 1985b; CIAT 1989). Severe attacks can kill young plants if the pest consumes all the buds. Such losses occur if the crop is 1 to 2 months old and suffers outbreaks of the pest, with more than four larvae per plant. These studies indicate that defoliation of plants younger than 5 months will reduce yield more than defoliation of plants aged 6 to 10 months.

Although each larva can consume 1107 cm^2 of leaf area, the cassava crop can tolerate relatively high populations. Under favorable environmental conditions, a crop can lose up to 80% of its leaves without reductions in root yield. Of the 1107 cm^2 of leaf area consumed during the larval period, about 75% is consumed during the fifth instar. At 15, 20, 25, and 30 °C, the average duration of the larval stage is, respectively, 105, 52, 29, and 23 days. This indicates that the hornworm's peak activity occurs at low altitudes (<1200 m) or during summer in the subtropics (Bellotti and Arias 1988).

Larvae vary in color: most commonly they are yellow, green, black (combined with small, lateral, white or red spots), dark gray, or cinnamon brown; occasionally, they are pink. Recently hatched larvae measure between 4 and 5 mm, and are mature between 12 and 15 days. In the fifth instar, they are 10 to 12 cm long. They drop to the soil where they pupate in a chitinous capsule that is brown with black streaks. Pupae are found in plant litter.

The adult emerges after 15 to 20 days, usually in the transitional periods between winter and summer or summer and winter. These outbreaks are irregular and years may pass without their occurring. Adults of *E. ello* are nocturnal. Females are a uniform ash color and males present a longitudinal black band in the forewings.

Eggs are olive green or yellow and large, having a 1.5-mm diameter. They are laid individually, preferably on the upper surface of cassava leaves. In pest outbreaks, eggs can also be found on lower leaf surfaces, petioles, and stems. In oviposition cages placed in the field (at 25 °C and 80% rh), females lived as long as 19 days, with an average of 8.6 days, while the male survived to a maximum of 15 days, with an average of 7 days. By day 6 or 7 after emergence, 50% of the adult population (i.e., T_{50}) had died. After a preoviposition period of 2 to 4 days, a female would oviposit a daily maximum of 500 eggs. Under confinement, a female may oviposit throughout her life, producing as many as 1800 eggs. Individual couples of moths may lay an average of 850 eggs while groups of couples may lay an average of 448 (CIAT 1978). These high oviposition rates, combined with the adults' migratory behavior, contribute to the rapid strengthening of hornworm populations and their sporadic appearance (Bellotti et al. 1992; Janzen 1987).

In the pupal state, females and males differ in the position of their genital openings. In the male, the genital opening (gonopore) is located in the ninth, enlarged, abdominal segment, leaving the eighth segment free. In the female, the genital opening is smooth and is found in the eighth segment, which is seen as a "V". The sex ratio is about 1:1, female to male.

This insect's great flight ability and migratory capacity, combined with its broad climatic adaptation and extensive host range (Janzen 1986, 1987) often makes effective control difficult. Pesticides may be adequate if the hornworm populations are detected and treated during the first three instars. However, farmers react to an attack of this pest by excessively applying insecticides outside appropriate times, thus triggering more severe attacks (Laberry 1997). A population of fourth and fifth instars is more difficult to control, but tolerating its presence is uneconomical because of the considerable defoliation they cause.

Applied pesticides also affect the populations of natural enemies, facilitating more frequent attacks from the pest (Urías-López et al. 1987). *Erinnyis ello* does have an associated complex of natural enemies, but its effectiveness is not significant, probably because of the adult's migratory behavior. A mass migration of adults causes a rapid imbalance between the pest and its natural enemies because they lay large numbers of eggs—at more than 600 per plant—in only 6 or 7 days in cassava fields. Accordingly, natural enemy populations are too low to prevent an outbreak of hornworm larvae and, thus, the crop's severe defoliation.

Because their reproduction rate is limited, parasites and predators cannot recover sufficiently fast to prevent the hornworm's dramatic outbreaks (Bellotti et al. 1992). Hence, two or three successive attacks may occur if outbreaks are not detected in time.

Adequate farming practices such as weed control and good soil preparation can reduce this pest's adult and pupal populations.

Biological control with parasitoids and predators. The key to effectively using biological control agents is synchronize the release of a large number of predators or parasites during the pest's early stages, preferably as eggs or as first to third instars. More than 40 species of parasites, predators, and pathogens of cassava hornworm eggs, larvae, and pupae have been identified (Bellotti et al. 1999):

- Eight microhymenopteran species belonging to the families Trichogrammatidae, Scelionidae, and Encyrtidae parasitize eggs of *E. ello*, for example, *Trichogramma minutum,* other *Trichogramma* spp.*, Telenomus sphingis, Tel. dilophonotae, Ooencyrtus* sp., and *O. submetallicus* (CIAT 1989). Some *Trichogramma* and *Telenomus* species have been reported as parasites for 94% to 99% of eggs (Bellotti and Schoonhoven 1978a).

- Dipteran parasitoids of this pest's larvae include the flies of the families Tachinidae (*Thysanomia* sp.), Sarcophagidae (*Sarcophaga* sp. and *Oxysarcodexia innota*), and Dryinidae (*Drino macarensis*). Hymenopteran parasitoids include wasps of the families Ichneumonidae (*Cryptophion* sp.) and Braconidae (especially *Cotesia* species [= *Apanteles*] such as *C. americana* and *C. congregatus*) Bellotti et al. 1992, 1994; Bellotti and Riis 1994).

- The most common egg predators are *Chrysoperla* spp. and *Chrysopa* sp. Other important larva predators are wasps (Hymenoptera: Vespidae) of the *Polistes* genus such as *P. erythrocephalus*; stink bugs *Podisus nigrispinus, P. obscurus*, and *Alceorhynchus grandis* (Hemiptera: Pentatomidae); and several spider species of the families Tomicidae and Salticidae (Bellotti et al. 1992).

The effectiveness of parasites and predators is curtailed by their limited functional response, which lasts about 15 days during a hornworm outbreak. Thus, for control to be successful, hornworm populations must be monitored in the field to detect immigrant adults or early instar larvae. This task requires traps with black light lamps (type BL or BLB, Ref. T20T12BLT) to attract flying adults or to help identify eggs or larvae (CIAT 1983b, 1989).

These light traps do not constitute a control method but function as a tool for discovering fluctuations in the abundance of adult *E. ello* populations. The data obtained permit better planning for applying different techniques to manage the pest. Preliminary trials led to the capture of 3094 adults in one night, mostly between 00:00 and 02:00. This information is highly useful for areas where no electrical power is available because traps run on batteries or gasoline can then be operated at those hours, thereby saving on resources. The difficulty is to synchronize a mass release of parasites and predators when a peak occurs in the pest population. Thus, there is need for an inexpensive and storable biological pesticide.

Biological control with microorganisms. Microbial control with sprays of *Bacillus thuringiensis* in doses ranging from 2 to 3 g p.c. per liter of water provides effective control. Effectiveness increases when larvae are within the first three instars (Arias and Bellotti 1977; Herrera 1999).

In 1973, CIAT found, in *E. ello* colonies, a virus that attacks the pest's larvae. The virus was identified at the University of California–Berkeley, USA, by Gerard M. Thomas as a baculovirus, which identification he reconfirmed in 1974 and 1977. CIAT then developed simple evaluation methods to discover how this virus could be used as a highly effective biological means for controlling the pest. Currently, this processed virus is the flag product for controlling hornworm as it can be applied conventionally and, moreover, stored for several years without its pathogenicity altering significantly.

At a commercial level, the viral compound was first developed and applied to large extensions of the cassava crop in Brazil, when larval populations were in first instar. The result was complete control. Later, in Venezuela, the virus was used instead of insecticides for large plantings (7000 ha) in areas where the hornworm was endemic. Dosage was 70 mL/ha applied to first- and second-instar larvae. Again, the result was complete control. The direct costs of storage, application, processing, and collection of larvae amounted to U$4/ha (CIAT 1995; Laberry 1997).

Fungal entomopathogens also exist, but any collection of affected insects in cassava crops was low. Of five sites evaluated, they were found in only one. Under laboratory conditions, a *B. bassiana* strain caused a 31.6% to 87.5% mortality rate in *E. ello*, with the third instar being the most susceptible. Fungal action is not transmitted from one generation to the next. When a *B. bassiana* strain was mixed with a *M. anisopliae* strain and applied to third instars, a 90% mortality rate was achieved without antagonism being presented. The dead larvae exhibited the typical symptomatology for each strain (Múnera S and De los Ríos 1999).

A fungus that attacks the pest's pupae was also identified. An ascomycete of the *Cordyceps* genus was very aggressive in the field, controlling the third outbreak of hornworm occurring in 1978 in the Department of Quindío, the only area where the fungus has been found. *Cordyceps* sp. can be easily reproduced on potato dextrose agar (PDA) and, when applied to pupae in the laboratory, achieves almost complete control.

Mechanical control. The manual collection of larvae and pupae is highly effective for reducing hornworm populations in small plantings. This practice is best applied to fields that the insect has only just begun to attack. When weeding tasks are carried out, digging the pupae up to the soil surface is sufficient for control, as they die from solar radiation or are destroyed with the hoe or weeding pole.

Cassava tiger moth caterpillar

This pest (*Phoenicoprocta sanguinea* Walker) belongs to the family Amatidae (also called Ctenuchidae) and is constantly found, although sporadically, within the cassava crop. Known as *bicho tigre* or "tiger bug" in Spanish, it defoliates the plant, although not at an economically significant level. However, it is considered as a potential pest of the crop, and has been reported in Colombia, Ecuador, Mexico, Brazil, and Suriname.

Biology and behavior. The adults of this species are moths of diurnal habit. They are small and showy. Their wing span measures 30 mm and the body is about 12 mm long. Females have black forewings, with the smaller hindwings having transparent areas. The abdomen is colored with metallic blue spots in the center of each abdominal segment. The bodies of males have blue, red, and yellow metallic spots on a black background. Both their forewings and hindwings are transparent (as typical of this family). The male is showier than the female, as it also has lateral red tufts on the abdomen, separated by central blue spots, and the thorax has yellow lateral tufts. The head is blue with black eyes.

The female lays eggs on the underside of leaves, preferably in the upper third of the plants. The eggs are semispherical, of a hyaline cream color, and measure about 1 mm in diameter. Eggs are laid individually, although sometimes in groups of 2, 4, or more eggs (up to 17). Incubation takes 4 to 5 days. The average number of eggs a female lays over 14 days is 192.

The larvae of *P. sanguinea* pass through five instars that together last 10 to 14 days. During this time, they also change colors, with each instar contrasting with the others. Larvae are covered with hairs that give them a furry appearance. The quantity and coloring of this "fur" varies according to instar. The first instars are a yellowish, almost translucent, fawn, becoming coffee-colored and gray until they acquire the red color of the fifth instar.

The first instar feeds in a circular fashion on the lower tissues of leaf blades, leaving an intact film of upper tissues. The film dries and later falls, leaving a circular perforation, which are often seen in mature crops and may join if many larvae eat the same leaf. Later instars uniformly consume the entire leaf, leaving only nervures. This action converts this insect into a potential crop pest. Evaluations of leaf consumption by *P. sanguinea* indicate that it can consume, on average, 78.5 cm^2 of leaf blade over its life cycle. This is 14 times less than that consumed by *E. ello* (Arias and Bellotti 1983). Larvae may measure between 2.6 mm (first instar) and 21 mm long (fifth instar) (Arias and Bellotti 1983).

After completing the fifth instar, the insect passes to the soil where it enters a prepupal state for 1 or 2 days before pupating in the soil litter, forming a cocoon with the setae or hairs of its body. The pupal state lasts 12 to 16 days. Pupae are coffee-colored and measure between 1.5 and 2.0 cm long, and between 0.5 and 0.7 cm wide. The insect's life cycle from egg to adult averages 41.2 days at 26 °C and 70% rh (Arias and Bellotti 1983).

Biological control. *Phoenicoprocta sanguinea* is a pest that, so far, does not require pesticides for its control because it has not yet presented outbreaks of economic importance. Control should, where possible, be through biological control agents that would maintain it at moderate to low levels in the field.

- Eggs of *P. sanguinea* are parasitized by *Trichogramma* sp. From each egg, five to eight small wasps emerge, at a gender ratio ranging from 0.5:1 to 5:1, female to male. In Ecuador, a small black wasp, not yet identified, was also observed to parasitize *P. sanguinea* eggs (B Arias and JM Guerrero 1999, pers. comm.).

- Larvae are parasitized by an *Apanteles* (= *Cotesia*) wasp, adults of which emerge when the pest larvae are in a prepupal state. Hence, *Apanteles* pupae can be seen developing within the cocoon formed by the pest larva. The cocoon thus becomes the wasp's puparium. From each puparium (cocoon) at least 6 to as many as 36 small *Apanteles* wasps emerge, at a sex ratio ranging from 1:1 to 23:1, female to male.

- An unidentified wasp, possibly of the Ichneumonidae family, was once observed in a typical parasitic pose over a pupa of the pest (Arias and Bellotti 1983).

Leafcutting Ants

In America, several ant species (*Atta* spp. and *Acromyrmex* spp.) have been reported as feeding on the cassava plant. An attack on the crop by a large population of worker ants can defoliate plants. The ants make semicircular cuts in leaves and, in severe attacks, buds. They take the cut parts to the anthill, where they then carry them below the soil surface. They then masticate the leaf parts to form a paste on which the fungus *Rhozites gongylophora* grows. The queen and ant larvae feed on this substrate.

Crop damage is usually evident as patches where plants appear defoliated, as when they are attacked by hornworm. However, ant damage differs from hornworm damage by the presence of semicircular cuts and of tracks that lead to anthills, which may be distant from the site of damage. Effects on yield are not known.

The most effective control is by insecticides. Anthills are easily recognized by the heaps of earth around entrances, and colonies can be destroyed by fumigating with smoke of either carbon disulfide or sulfur.

- Lorsban, applied periodically to nest entrances with a blower, is effective for reducing ant populations.

- An economic and ecological control is to attack the fungus that feeds the queen. To achieve this, the pH of the anthill is changed by periodically applying lime to the entrances and within the anthill with a blower (G Sotelo 2000, pers. comm.).

- Lime and Lorsban, mixed at a ratio of 2:1, can also be applied. This will attack both fungus and ants.

An important crop management practice is to determine the time of the queens' nuptial flights and capture them as they begin nest construction. This can be identified by small open orifices in the soil, which have the earth around them removed by the queens on initiating the new colonies. In some parts of the Department of Cauca, young schoolchildren are taught to recognize these small nests and are paid according to the number of queens they collect. In some indigenous areas, these queens are collected as food.

Leaf-Sucking Mites

Mites are a universal pest of cassava plants, causing serious losses in crops in America and Africa (Herren and Neuenschwander 1991; Bellotti et al. 1999). More than 40 species have been reported as feeding on cassava foliage (Byrne et al. 1983), the most frequent of which are *Mononychellus tanajoa* (syn. *M. progresivus*), *M. caribbeanae*, *Tetranychus cinnabarinus*, and *T. urticae* (also recorded as *T. bimaculatus* and *T. telarius*) (Bellotti 2000a, 2000b).

The cassava crop is the principal host of the *Mononychellus* complex. In contrast, the *Tetranychus* complex has a broad range of hosts. Other mite species (e.g., *Oligonychus peruvianus, O. biharensis, Eutetranychus banksi*, and *M. mcgregori*) have little economic importance because they feed on cassava foliage only sporadically (Byrne et al. 1983; Bellotti 2000a). In almost all cassava-producing regions of the world, mites frequently attack the crop during dry seasons, causing severe damage.

The mite *Tetranychus urticae* is universally widespread and is considered the most important pest in some areas of Asia. The distribution of *O. peruvianus* is limited to America. When environmental conditions are optimal, mites are found in large numbers on the underside of cassava leaves.

Mononychellus tanajoa Bondar or the cassava green mite (CGM)

Although this species is native to America, it has considerably reduced crop yield in several parts of East Africa after its introduction to that region and its dissemination to other areas of the African continent.

Mononychellus tanajoa is usually active around the plants' growing points, buds, young leaves, and stems. The central and lower parts of the plant are less affected by this species. In severe attacks, shoots lose their green color, and leaves show yellow points uniformly distributed throughout the surface, so that the leaves acquire a mottled and bronzed appearance, as if suffering from a mosaic. Leaves are also small and deformed (Byrne et al. 1983).

Stems become scarred, rough, and brown. Sometimes they suffer dieback, that is, a progressive necrosis from the plant's upper parts to its lower parts. Terminal points become lancet-shaped through the loss of leaves and possess a cork-like appearance. Re-shooting can occur but if rains are scarce, the new leaf shoots may also be attacked (Yaninek and Animashaun 1987). If the rains return, tolerant varieties may recover their foliage. An important characteristic of the uniformly green *Mononychellus* mite is that it does not produce webs to disperse from one plant to another.

Tetranychus urticae Koch or the red spider mite

The damage caused by this mite first appears in leaves of the central and lower parts of the plant. Initially, a yellowing appears in the area of convergence of the central nervures of leaf folioles and where the mite populations concentrate. The yellow points then extend throughout the central nervures and become scattered throughout the whole leaf, which then takes on a reddish or rusty brown color. The basal leaves are the first to be affected. Heavily infested leaves dry up and fall. Under normal conditions, the upper parts of plants are green while the central and lower parts are affected or defoliated. In severe drought, this mite can invade entire plants, killing them in susceptible varieties.

This species produces webs to move from one part of the plant to another or between neighboring plants. Like *M. tanajoa*, the mites are green, but differ by being a little larger and presenting on each side of the body a dark spot that is observable only under the microscope.

Tetranychus cinnabarinus Boisduval or the carmine spider mite

This reddish-colored mite produces symptoms similar to those of *T. urticae.*

Oligonychus peruvianus McGregor (flat cassava mite)

In the plant, the pest manifests as small white spots on the underside of leaves. The spots are webs that the females construct, commonly on central, secondary, tertiary, and leaf marginal nervures. Oviposition occurs under the webs, where the immature stages of the mite feed and develop. As adults, the mites abandon the webs to form new colonies. In each web, 5 to 10 mites are found. On the upper surface of leaves, small, brown, irregular, and necrotic areas form, corresponding to the feeding activities of each colony on the leaves' undersides. Colonies usually form in the plant's central and lower parts. When environmental conditions are favorable and if the cassava variety is susceptible, the entire plant can be invaded.

Yield losses caused by mites

Economically, the CGM is the most important mite species, with losses of cassava crops being reported in the Americas and Africa (Herren and Neuenschwander 1991; Bellotti et al. 1999), especially in dry seasons in tropical lowlands (Yaninek and Animashaun 1987; Braun et al. 1989). Nyiira (1972) reported that, in Africa, reductions of yield caused by *M. tanajoa* were as much as 40%; and Bellotti (2000b) estimated that yield losses in Venezuela were 30% to 40%.

In field trials with young crops, reductions were 21%, 25%, and 53% during 3, 4, and 6 months of attack, respectively (Bellotti et al. [1983c]). Under field conditions, a high mite population reduced yields by 15% in a resistant material, 73% or more in a susceptible material, and 67% in planting materials (Byrne et al. 1982, 1983; Bellotti 2000a, 2000b).

The *M. tanajoa* mite was originally found in Northeast Brazil, in 1938. It appeared for the first time in Africa (Uganda) in 1971 and, by 1985, it was dispersed throughout the continent's entire cassava-growing belt, involving 27 countries (Yaninek 1988). Losses ranged from 13% to 80% (Yaninek and Herren 1988; Herren and Neuenschwander 1991; Skovgard et al. 1993; Bellotti 2000a).

Controlling pest mites

Research on the control of *M. tanajoa* has taken two principal directions: host-plant resistance (HPR) and biological control. These two complementary strategies help reduce CGM populations and thus its level of economic damage. Continuous use of acaricides is not an economical option for low-income farmers. Nor are these products recommended because they cause adverse effects on the pest's natural enemies (Bellotti 2000a).

Host-plant resistance. Significant work has been conducted in cassava improvement by two international research centers (CIAT and IITA) and several national research programs, including the National Cassava and Fruits Research Center (CNPMF, coordinated by the Brazilian Agricultural Research Corporation or EMBRAPA, its Portuguese acronym). All had tried to develop hybrids with resistance to CGM (Byrne et al. 1983; Bellotti et al. 1987; Hershey 1987). About 5000 cassava varieties held in the germplasm bank at CIAT were evaluated for their resistance to CGM and the other mites mentioned above. Results indicated that about 6% (300 varieties) possessed low levels of resistance or tolerance of the *Tetranychus* genus, and moderate levels of resistance to the genera *Mononychellus* and *Oligonychus* (CIAT 1999). This basic work enabled the development of varieties with moderate levels of resistance. These varieties were then released to farmers (Arias and Guerrero 2000).

Research carried out by CIAT on cassava resistance to CGM was traditionally conducted at two sites:

- CIAT–Palmira, located in the intermediate Andean area, at 1000 m above sea level, where mite populations are moderate (Arias and Guerrero 2000).

- Pivijay (Magdalena), in the Colombian Atlantic Coastal Region, located in the tropical lowlands. This area is characterized by a dry season of 4 to 6 months and high mite populations (Arias and Guerrero 2000).

The cultivars selected had low to moderate levels of resistance, scoring damage values between 0 and 3.5, according to a scale of 0 to 6 (Arias and Guerrero 2000), where 0 was no damage and 6 was severe damage.

Of the 300 varieties selected as promising for durable resistance (2 to 7 cropping cycles), 72 maintained a score for damage of less than 3.0 (CIAT 1999). Most of these varieties were collected in Brazil, Colombia, Venezuela, Peru, and Ecuador. Some were hybrid (Arias and Guerrero 2000).

Mechanisms for resistance to the mite were interpreted as comprising either antixenosis (where the plant repels insects by morphological means, e.g., pubescence) or antibiosis (where the plant adversely affects insect physiology, e.g., through chemical means) (Byrne et al. 1982). Mites feeding on susceptible varieties develop fast; are highly fecund; readily accept the plant; and have a long life span as adults, and low larval and nymphal mortality rates. Those that feed on resistant materials, however, do not behave this way (Byrne et al. 1983). Instead, they have high mortality rates, long developmental periods, and less oviposition over shorter periods. Recent laboratory studies show *M. tanajoa* as strongly preferring to oviposit on susceptible varieties. When resistant varieties M Ecu 72, M Per 611, and M Ecu 64 were compared with the susceptible CMC 40 (M Col 1468) in a free-choice test, preference for the susceptible variety was 95%, 91%, and 88%, respectively (Arias and Guerrero 2000).

Biological control. Studies were carried in numerous cassava fields, with the experimental data indicating that, despite being present in Neotropical lowlands, CGM attacks rarely cause significant losses, except in some areas of Brazil. Consequently, a work-in-progress, which extended from 1983 to 1990 and covered 2400 sites in 14 countries of the Americas, was conducted to evaluate the complex of the CGM's natural enemies (Byrne et al. 1983; Bellotti et al. 1987).

A reference collection of CGM predators, developed by CIAT and Brazil, is now held at CIAT. It includes the acarophagous mites, known as *phytoseiids*, found on cassava (Table 10-2). It also lists the various geographical areas chosen for collection because of their ecological similarity with sites in Africa and Brazil with mite problems. Of the 87 collected and stored predatory species, 25 were new or had not been recorded before and 66 species (76%) were collected from cassava crops. A taxonomic key of phytoseiid species associated with cassava was then prepared as part of a collaborative project with several Brazilian colleagues. The CIAT–Brazil collection has a database that can be easily used for describing or re-describing species, listing mite types and paratypes.

Of the 66 species of phytoseiids collected from cassava plants, 13 were the most common, including *Typhlodromalus manihoti*, which was the most frequently collected species, being found in more than 50% of sampled fields. This species was followed by *Neoseiulus idaeus*, *T. aripo*, *Galendromus annectens, Euseius concordis*, and *E. ho*. Phytoseiids *T. aripo* and *N. idaeus* are promising biological control agents for *M. tanajoa* in Africa (Yaninek et al. 1991, 1993).

The explorations revealed other insects as predators of the CGM, particularly the staphilinid *Oligota minuta* and the coccinellid *Stethorus* sp. The phytoseiids and other predators were carefully studied in the laboratory and field (Table 10-2), with the phytoseiid mites being verified as more efficient than the predatory insects (Byrne et al. 1983).

Table 10-2. Biological and ecological aspects of phytoseiids that prey on cassava mite pests.[a]

Phytoseiid predator	Colonies (no., 1986–1999)	Relative humidity	Consumption of *Mt* eggs (24 h)	Growth period (days)			Fecundity			Females			
										Longevity		(%)	
				Mt	*Tu*	*Mc*	*Mt*	*Tu*	*Mc*	*Tu*	*Mc*	*Mt*	*Tu*
Typhlodromalus manihoti	31	+	68.0	4.9	4.1	5.5	14.2	—	3.5			74	88
T. aripo	9	+				6.8		13.0	13.0	14.0	20.9		
T. tenuiscutus	7	+	45.4	5.8	5.8	5.7	32.0	2.5	16.1	6.6	16.1	75	81
T. rapax	1			5.0	5.4	5.8	6.0	12.0	19.4			78	62
Neoseiulus idaeus	20	+++	26.8	4.6	4.6	5.1	13.8	32.3	12.5	21.6	27.8	73	84
N. californicus	5	++	26.5	4.7	4.4	7.7	34.8	43.7	23.4			70	79
N. anonymus	4			4.7	5.1	5.2	14.5	34.4	27.7	39.1	12.0	73	58
Galendromus helveolus	5	+		7.4	7.0		18.7	8.0	23.0	14.2	19.0	64	66
G. annectens	6	++	17.8	5.7	6.1		22.4	19.0	31.0	23.0	27.7	74	85
Euseius concordis	1		5.7	5.0			12.7					75	70

a. Relative humidity: + = 75%; ++ = 60%; +++ = 40% to 50%; *Mt = Mononychellus tanajoa; Tu = Tetranychus urticae; Mc = Mononychellus caribbeanae.*

The results of these studies showed that CGM density was higher in Northeast Brazil than in Colombia and that the diversity of phytoseiid species was considerably higher in Colombia than in Brazil. Of the fields evaluated in Colombia, 92% were either not infested with the mite pest or were infested at very low densities (i.e., at less than 25 mites per leaf). In contrast, for crops in Brazil, only 12% of fields were not infested and 25% had intermediate or high densities of CGM (Bellotti et al. 1994).

Results of field experiments in Colombia (Braun et al. 1989) demonstrated the importance of the effect of various phytoseiid species associated with CGM. In Colombia, fresh and dried root production dropped by 33% when natural enemies were eliminated. In comparison, acaricide applications did not increase production, thus indicating that the biological control was good.

Since 1984, numerous phytoseiid species were sent to Africa from Colombia and Brazil. Of the mass-released species, none from Colombia became established, but three species from Brazil (*T. manihoti, T. aripo*, and *N. idaeus*) managed to become established (Yaninek et al. 1991, 1993; Bellotti et al. 1999). Of the three, *T. aripo* seems the most promising, as it dispersed rapidly and, today, is found in more than 14 countries. Field evaluations indicate that *T. aripo* reduces the CGM population by 35% to 60%, resulting in increases of fresh matter production by 30% to 37%.

Neozygites sp. *cf. floridana* (Zygomycetes: Entomophthorales), a pathogenic fungus, causes irregular or periodic mortality in mite populations in Colombia and Northeast Brazil (Delalibera Jr et al. 1992). This pathogen was found in many cassava fields in several Neotropical regions. Some strains were specific to the *Mononychellus* genus (de Morães et al. 1990), and was also found on CGM in Africa, although no epizootics of the fungus were observed (Yaninek et al. 1996). The fungal strain from Brazil may therefore be more virulent than that from Africa. Molecular techniques are currently being used to taxonomically identify the strains and *in vitro* methodologies are being developed to produce the pathogen. This fungus, which appears highly promising for the biological control of CGM, is also being evaluated in Africa.

Leaf-Sucking Insects

Cassava whiteflies

Whiteflies (Hemiptera: Aleyrodidae) feed directly on the cassava plant and also serve as vectors of viruses that attack the crop. They therefore cause significant damage to this crop in the agroecosystems of America, Africa, and, to a lesser extent, Asia. The Neotropical whitefly complex is enormous, with 11 species recorded as associated with cassava (Bellotti et al. 1994, 1999; Castillo 1996; França et al. 1996):

Aleurotrachelus socialis Bondar
Trialeurodes variabilis Quaintance
Bemisia tuberculata Bondar
Aleurothrixus aepim Goeldi
B. tabaci Gennadius
B. argentifolii
Trialeurodes abutiloneus Haldeman
Aleurodicus disperses Russell
Paraleyrodes sp.
Aleuronudus sp.
Tetraleurodes sp.

Aleurotrachelus socialis is the predominant species in northern South America, where it causes considerable damage to crops. It is also found in Brazil, although in smaller numbers (Farias 1994). Small populations of *B. tuberculata* and *Trialeurodes variabilis* have been reported in Brazil, Colombia, Venezuela, and other countries (Farias 1990; Bellotti et al. 1999). The spiralling whitefly (*Aleurodicus dispersus*) causes damage to cassava in western Africa (Neuenschwander 1994b; D'Almeida et al. 1998). In Colombia, small populations of this species have been found in cassava crops of the Atlantic Coast and Valle del Cauca. This whitefly also appears in some provinces of Ecuador (B Arias and JM Guerrero, pers. comm.). *Bemisia afer* has been found in Kenya (Munthali 1992) and Côte d'Ivoire (Bellotti 2000a, 2000b).

Biology and behavior. Whitefly *B. tabaci* is distributed throughout the tropics, feeding on cassava plants in Africa and various regions of Asia, including India (Lal and Pillai 1981) and Malaysia. In 1990, *B. tabaci* biotypes in America were found feeding on cassava. These whiteflies are known to transmit viruses that cause the following diseases in cassava:

- African cassava mosaic disease (ACMD), caused by several geminiviruses transmitted through *B. tabaci* (Thresh et al. 1994; Bellotti 2000a).

- Frogskin disease, which affects cassava in the Neotropics maybe transmitted by *B. tuberculata* (Angel et al. 1990; Bellotti 2000a).

The absence of ACMD in the Americas is believed to be related to its vector's (*B. tabaci*) inability to colonize cassava. At the beginning of the 1990s, a new *B. tabaci* biotype (B), which some consider as a separate species (*B. argentifolii*), was found in the Neotropics feeding on cassava. African cassava mosaic disease is now believed to be a serious threat to cassava production in the Neotropics, as most traditional cultivars of this region are highly susceptible to the disease. Furthermore, the biotype complex of *B. tabaci* comprises vectors of several viruses that affect cultivated species that are often grown in association with cassava or in adjacent fields. The possibility that viral diseases will circulate between these species or that new viruses will appear represents a potential threat to cassava production (Bellotti 2000a, 2000b).

Females of *A. socialis* oviposit individual banana-shaped eggs on the underside of apical leaves. Incubation takes about 10 days and the insect undergoes three nymphal instars and a pupal phase (fourth instar) before reaching the adult stage. During the third instar, the body changes from a cream color to black and is surrounded by a waxy white layer. The black pupae make this species easy to distinguish from other whitefly species that feed on cassava. Development from egg to adult in an incubator is 32 days at 28 ± 1 °C and 70% rh (Arias 1995). Studies on oviposition in *A. socialis* indicate that a female lays as many as 224 eggs (Bellotti 2000b).

A female *Trialeurodes variabilis* oviposits, on average, 161 eggs that have a 62% chance of survival from egg to adult. The female lays the bullet-shaped eggs vertically, as do the *B. tuberculata* and *B. tabaci* females. The average longevity of females was 19.2 days and that of males 8.8 days. Pupae of the *Bemisia* species are oblongate and are normally pale green. Consequently, to differentiate the morphological characteristics of each species, microscopy should be carried out and differences taken into account.

High populations of *T. variabilis* are usually associated with the rainy season when plants are more vigorous. However, population levels may depend more on the plant's physiological conditions than on the climate.

Damage and losses. Whiteflies directly damage leaves through their feeding activities. Both adults and immature states of *A. socialis* are active and destructive. They feed on the phloem, the females even feeding while copulating and ovipositing. This behavior produces chlorosis and cone-like rolling of bud leaves. In susceptible varieties, leaves of the central third of plants, where nymphs are found, are reduced in size and present yellowing from the margins towards the center, together with corrugated areas that are greener than others, thus giving the leaves a mosaic appearance. These leaves usually become yellow, necrose, and eventually fall off.

Depending on the intensity of the attack, they may also become covered by the sooty black growth of a fungal complex known as *fumagina* sooty mold (Arias 1995). In susceptible varieties, especially if attacks start early in the crop's development and last until the late stages of vegetative growth, the plants become rachitic and their thin stems suffer from lodging. Re-shooting therefore occurs, but these shoots are also palatable to the adult pest. The pest thus succeeds in affecting the production of planting materials, crop yield, and quality of harvested roots (Arias 1995).

Populations. Research carried out in the Neotropics has concentrated on *A. socialis* and *Aleurothrixus aepim*. Populations of both species increase during dry seasons, but may be presented throughout the cropping cycle (Farias et al. 1991; Gold et al. 1991). In the Department of Tolima, during summer, *A. socialis* populations increase, wheareas those of *T. variabilis* diminish. In the rainy seasons, the reverse occurs, with the *T. variabilis* populations being high and those of *A. socialis* low (Bellotti 2000a, 2000b).

In the latter half of the 1990s and the first semester of 2000, *A. socialis* populations increased considerably, becoming endemic in the Departments of Cauca and Valle del Cauca and seriously affecting the farming economy of those areas. Populations of this whitefly remained constant both in dry and rainy seasons. Apparently, rainy days alternating with days of strong sun and high temperatures favor and stimulate the incidence of this pest, which even impede the presence of other pests (B Arias and AC Bellotti 1998, pers. comm.). Prolonged attacks of this pest on a crop may affect the capacity of stakes to shoot (G Jaramillo 1999, pers. comm.).

Production losses caused by *A. socialis* and *Aleurothrixus aepim* are common. The duration of an attack by whitefly correlates with losses in cassava root production. Attacks by *A. socialis* over 1, 6, and 11 months resulted in 5%, 42%, and 79%, respectively, of losses in root yield in field trials conducted by CNIA–Nataima of CORPOICA, in the Department of Tolima, Colombia (Vargas H and Bellotti 1981; Bellotti et al. [1983c], 1999).

Whiteflies management. Various methods are used to control the pest, including pesticides, cultural control, varietal resistance (i.e., HPR) and biological control. The last two have been increasingly accepted to complement other pest control practices. A more traditional approach is crop management. These three approaches help reduce environmental pollution and other disadvantages that excessive use of chemical pesticides presents.

In the Neotropics, research initially focused on controlling whitefly in cassava crops through HPR activities and crop practices. More recently, considerable work has been conducted on identifying natural enemies and evaluating their actions in the context of integrated pest management (IPM) (Bellotti 2000a).

Farming practices, including traditional systems of intercalating the cassava crop with other crops, also help reduce pest populations (Leihner 1983), as follows:

- Egg populations of *A. socialis* and *T. variabilis* in a cassava/cowpea association were lower than those in crops under monoculture (Gold et al. 1990). The effects were residual, persisting for 6 months after harvest. Production losses in a cassava/maize association, a cassava monoculture, and a mixed cropping system were about 60%. In contrast, production losses in a cassava/beans system were only 12% (Gold et al. 1989b, 1989c). However, the cassava/maize association did not reduce egg populations (Gold 1993). Thus, the success of this technique depends on the crop species being intercalated, which limits effectiveness and acceptability to farmers. With the right crops, however, it can reduce pest populations in small-farmer crops (Bellotti 2000a).

- For agronomic control, the management of planting dates plays an important role in reducing pest incidence. If planted in a suitable rainy season, the crop can be free of the pest, or needs to support only small populations, in the first 2 to 3 months of vegetative growth, which are significant for crop development. Timely weed control and fertilizer applications (where necessary) will also prevent competition with other plants, giving the crop plants an initial vigor that will enable them to support attacks from this insect (Arias 1995).

- Researchers use yellow traps to physically control whiteflies in different crops. The pest is attracted by surfaces that reflect yellow in the range of 500 to 700 nm (Berlinger, cited by Arias 1995).

Control by varietal resistance (HPR). Varietal resistance offers a stable option that is low-cost and long-lasting in the control of whitefly populations. Resistance to whitefly is rare in crops, although good sources of resistance have been identified and highly productive resistant hybrids are being developed. The HPR studies initiated at CIAT more than 15 years ago have systematically evaluated more than 6000 cassava varieties from the germplasm bank for resistance to whitefly (CIAT 1999), especially to *A. socialis*. In Brazil, research was carried out with *Aleurothrixus aepim* (Farias 1990a, cited by Arias and Guerrero 2000).

Various sources of resistance to *A. socialis* have been identified. The cassava clone M Ecu 72 has consistently shown high levels of resistance. Other varieties presenting moderate to high resistance include M Ecu 64, M Per 335, M Per 415, M Per 317, M Per 216, M Per 221, M Per 265, M Per 266, and M Per 365. These results suggest that resistance to *A. socialis* is found in germplasm native to Ecuador and Peru, but more research is needed. Materials M Ecu 72 and M Bra 12 (agriculturally desirable clones that tolerate whitefly in the field) were used in an improvement program to increase the production and resistance of clones that showed no significant differences in production when grown in either plots treated with insecticides or untreated plots (CIAT 1992; Bellotti et al. 1999).

Greenhouse and field studies showed that *A. socialis*, after feeding on resistant varieties, oviposited less, developed more slowly, were small, and suffered a higher mortality rate than those that fed on susceptible clones. First-instar nymphs of *A. socialis*, after feeding on M Ecu 72, presented a 72.5% mortality rate (CIAT 1994; Arias 1995) (Figure 10-1). Selected progenies (CG 489-34, CG 489-4, CG 489-31, and

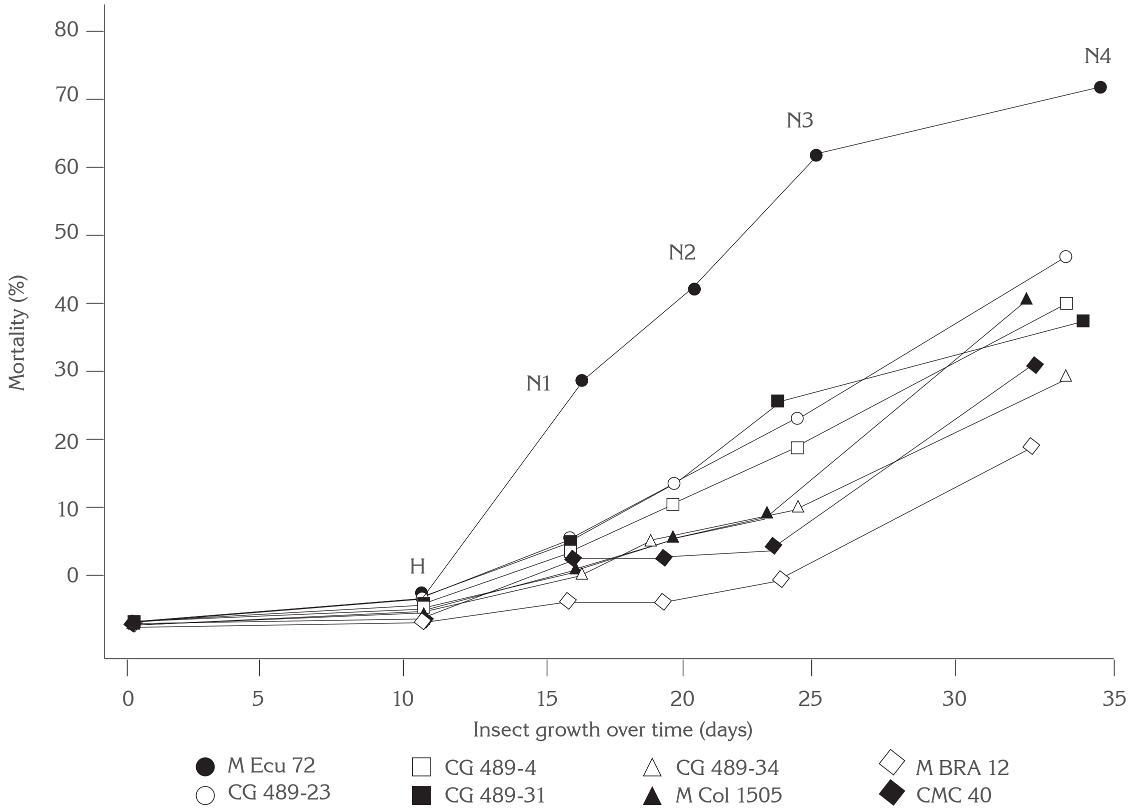

Figure 10-1. Mortality of whitefly *Aleurotrachelus socialis* with respect to its stage of development on cassava clones that are either resistant or susceptible to the pest. H = hatching, N1 = nymph 1, N2 = nymph 2, N3 = nymph 3, N4 = nymph 4.

CG 489-23) of a cross between M Ecu 72 and M Bra 12 had moderate levels of resistance to whitefly. Three of these hybrids are currently being evaluated for release to Colombian farmers in the Department of Tolima, Colombia (Arias and Guerrero 2000).

In Colombia, field evaluations of resistance to natural populations of *A. socialis* have been conducted at two sites:

- In Nataima, Tolima, in cooperation with the Colombian Corporation of Agricultural Research (CORPOICA). Populations of *A. socialis* found in Nataima have been at moderate to high levels in the last 15 years. Hence, long-term research is possible there (Arias and Guerrero 2000).

- In CIAT–Palmira, Valle del Cauca. Initially, the *A. socialis* population was low. However, since 1994, it has increased and is currently higher than it is in Tolima. This sudden increase is not yet understood but the dynamics show an outbreak of this pest in a crop that had previously supported its attacks (Arias and Guerrero 2000).

CIAT is currently conducting research to identify markers linked to genes that confer resistance to *A. socialis* attacks to understand the genetics of resistance in cassava to whitefly in preparation for field evaluations.

Building a 10-cM framework map for QTL analysis and identification of candidate genes for whitefly resistance (WF^R) in cassava

Cassava genetic and genome resources. Cassava is an allopolyploid with 36 chromosomes (Magoon et al. 1969). Due to poor seed set, the heterozygous nature of the crop, the high genetic load, and the high susceptibility to inbreeding depression on the loss of heterozygosity, shoot cuttings, thereby preserving its heterozygous nature, propagate most cassava. This heterozygosity provides challenges to cassava breeders but has enabled the identification of over 600 molecular markers (Blair et al. 2007). Simple sequence repeat (SSR) markers were used to study the genetic diversity and structure in a large collection of local varieties from Africa and Latin America. CIAT constructed the first linkage map of cassava (Fregene et al. 1997). Since then molecular markers have been linked to the single genes conferring resistance to CMD, green mites, and cassava bacterial blight (CBB), enhanced ß-carotene content, and early root yield (Ferreira et al. 2008; Marín Colorado et al. 2009; Ogunjobi et al. 2006). The above resources are available at cassava database housed at CIAT.

The draft cassava genome (CIAT line AM560-2) was released by the U.S. Department of Energy-Joint Genome Institute (DOE-JGI) under the Community Sequencing Program (www.jgi.doe.gov/CSP). Currently, the Gates Foundation has invested $1.3 M to refine the genome annotation and develop a robust SNP resource to enable molecular mapping in cassava (CGP 2009). Over 47,000 protein-coding loci are currently annotated on the cassava genome and 24,388 of these loci are supported by ESTs (CGP 2009). Two additional full-lenght cDNA libraries were constructed more recently and are being analyzed (CIAT/RIKEN). These libraries contain cDNAs from over 23 treatments including *A. socialis* infestation of MEcu72 (WF^R) leaves.

Genetic linkage maps are a prerequisite to studying the inheritance of both qualitative and quantitative traits (Morgante and Salamini 2003). To identify the mechanisms of WF^R in cassava, we are determining the heritability and the number of loci that contribute to the antibiotic and antixenotic resistance expressed in MEcu72. To this end, it is necessary to construct a 10-cM framework linkage map for MEcu72 using statistically well-supported EST, AFLP, SSR, and SNP markers. Cassava is a highly heterozygous species with strong inbreeding depression (Blair et al. 2007). Homozygous lines cannot be obtained and F_2 populations often suffer from genetic bias induced by the death of some genotypes. For this reason, F_1 plants are used in cassava mapping. We are using 184 F_1 progeny from a cross between MEcu72 (♀ WF^R) x MCol2246 (♂ WF^S). This population size increase LOD score estimation and hence facilitate the identification of WF^R QTL(s) explaining more than 5% of the phenotypic variance. A second F_1 segregating population with 200 individuals from the cross between MEcu72 (♀ WF^R) and CMC40 (♂ WF^S) will be used to validate the markers flanking the QTLs explaining the largest phenotypic variance.

Unravel the genetic mechanism of WF^R using association genetics. Our 10-cM framework map will be used for the identification of WF^R QTLs using composite interval mapping, which is based on mixture models and maximum-likelihood techniques. These analyses will allow us to identify the major and minor QTLs conferring WF^R. For molecular markers to be useful for integrating WF^R into WF^S varieties used by smallholder farmers, the markers must be validated in a second mapping population (MEcu72 x CMC40). At the end of this project period, we will be poised to initiate MAS breeding to incorporate WF^R into cassava lines preferred by smallholder farmers using the SNP/SSR markers linked to the WF^R QTLs, which contain quantitative resistance (*QR*) gene(s) that confer WF^R.

Identification of candidate genes for resistance to whitefly using microarrays. Microarrays technology and subtractive libraries were used to identify differentially expressed genes in cassava during *A. socialis* attack (Bohórquez 2011). These methodologies allowed us to identify 405 sequences induced by *A. socialis* in all stages of their life cycle. These sequences are involved in biological process like defense, cell wall modification, oxidative burst, signal transduction, transport, primary metabolism, and photosynthesis. Some of these sequences are part of the signaling pathways regulated by jasmonic acid (JA) and ethylene (ET), which are involved in defense response to pathogens and herbivores. When *A. socialis* feeding on leaves of genotype MEcu 72, introduce their stylet, and insect-derived elicitor (salivary components and/or chitin) are recognized by a plant receptor. In the case of chitin, it is proven that the family of transcription factors *AP2/ERF* are induced by chitin, which is a component of the insect exoskeleton. This transcription factor is induced by the signaling cascade that begins with plasma membrane depolarization and Ca^{2+} flow, then are activated MAPK signaling cascades and subsequent induction of phytohormones pathways such as JA/ET. *AP2/ERF* transcription factors are potential mediators of the synergistically induction process between JA and ET and induce defense genes such as basic vacuolar proteins *PRB1, CHIB (PR-3),* as well as lectins and proteinase inhibitors. These proteins can have several effects against insects, such as poisoning, may target components of the insect gut that contain carbohydrates, can inhibit the action of proteases preventing whiteflies to digest their food well, dying of malnutrition. The defense response is complex and involves all the processes of cellular metabolism, some of which themselves can be effector mechanisms that are controlling the attacker. Among these are the generation of ROS, which produces enzymes that can affect insect diet or inducing plant hormone signaling pathways mentioned above. Cell wall modification, which may make it difficult to insect feeding and may also mediate the defense response regulated by JA/ET, and finally the protein degradation machinery in which are various proteases with different roles involved in defense against pathogens. At the same time, the plant represses its primary metabolism and photosynthesis, reallocating C and N resources to the defense.

The application of functional genomics approach in the study of cassava defense responses, opens a wide range of future applications at different levels, both *in silico* and experimentally. Gene expression analysis, construction of physical and genetic maps, genomic sequence analysis, gene silencing, and production of genetically modified organisms are some of the projects will be developed in the future.

Biological control. In explorations carried out recently in the Neotropics—especially in Colombia, Venezuela, Ecuador, and Brazil—numerous species of natural enemies have been identified as associated with the whitefly complex that attacks cassava. Not much is known of the complexes of natural enemies associated with the different whitefly species. Thus, we cannot readily determine each complex's effectiveness and its potential in biological control programs. We know sets of parasitoids exists, but little is known about these insects' levels of parasitism, rates of parasitism per whitefly species, the specific hosts that are chosen, and their effects on the regulation of whitefly populations.

Since 1994, CIAT researchers have conducted explorations to identify natural enemies in northern South America. The most representative group is that of the microhymenopteran parasitoids (Castillo 1996; Evans and Castillo 1998). An abundance of these species exist in Colombia. More than 10 species, some not even recorded, were collected, but the genera that most frequently associated with *A. socialis, B. tuberculata*, and *T. variabilis* were *Encarsia* (especially *E. hispida* and including *E. pergandiella* and *E. bellottii*), *Eretmocerus* (species not yet identified), and *Amitus* (including *A. macgowni*) (Castillo 1996; Evans and Castillo 1998).

The highest levels of parasitism observed in *A. socialis, B. tuberculata*, and *T. variabilis* were 15.3%, 13.9%, and 12.1%, respectively, and varied according to geographical region (Castillo 1996). Parasitism was higher in the Andean Region than in the coastal and flat regions of eastern Colombia.

Studies conducted in Colombia during 1997 to 1999 showed that *Encarsia* was the most frequently collected genus in the Andean Region and that *Eretmocerus* predominated in the low altitudes of the Caribbean Coast (CIAT 1999). Parasitoid species associated with each whitefly species may be influenced by geographical region. In Valle del Cauca (1000 m above sea level), 99.6% of parasitism of *A. socialis* was from *Encarsia* and 0.4% from *Eretmocerus*. The most numerous species in the parasitoid complex was found in association with *B. tuberculata*.

Greenhouse studies on *E. hispida* as a parasite of *A. socialis* show that the third instar of whitefly is the preferred. Parasitism rates on different instars were 15.6%, 44.7%, 75.3%, and 43.1% on the first, second, third, and fourth instars, respectively. The average rate of parasitism was 45%, with the highest levels being between 72 and 96 h after exposure (CIAT 1999; Ortega 2000). *Encarsia hispida* is the parasitoid most frequently seen when *A. socialis* populations are high. However, its effectiveness in regulating whitefly populations in the field is not known.

The way in which cassava varieties resistant to *A. socialis* influence parasitoid behavior has also been evaluated. The survival of *E. hispida* was not negatively affected by resistant cassava genotypes. However, fewer parasitoids emerged from pupae of *A. socialis* whose larvae had previously been fed with resistant variety M Ecu 72 than from pupae of larvae fed on susceptible variety CMC 40 (CIAT 1999).

During December 2000 and the first 3 months of 2001, a large number of the parasitoid *Amitus macgowni* was observed at the CIAT–Palmira experiment station in high populations of *A. socialis*. Between 20 and 80 examples were captured per leaf and more than 2500 per hour (B Arias 1998, pers. comm.).

Three fungal entomopathogens that attack whitefly on a world level have been tried in the laboratory: *Beauveria bassiana, Verticillium lecanii*, and *Metarhizium anisopliae*. Although these fungi have not been found in Colombia as natural parasites, *B. bassiana* was observed to cause mortalities of 28%, 55%, and 39% in first, second, and third instars of *A. socialis*, respectively. The second instar was the most susceptible under laboratory conditions. *Beauveria bassiana* and *M. anisopliae* also caused mortality rates of 18.1% and 18.8%, respectively, when introduced in the morning, and 12.4% and 5.7% when introduced in the afternoon (Sánchez and Bellotti 1997).

Lace bugs

Lace bugs (Hemiptera: Tingidae) attack cassava in several South and Central American countries. These bugs are a pest in the Neotropics, but have not been reported in Africa or Asia. Froeschner (1993) identified several species, of which the most important for cassava are *Vatiga illudens*, *V. manihotae*, and *Amblystira machalana*. *Vatiga manihotae* is found mainly in Colombia and Venezuela, but is also found in Cuba, Trinidad, Peru, Ecuador, Paraguay, Argentina, and Brazil. *Vatiga illudens* predominates in Brazil, but is also found in the Caribbean Region. Black lace bug, *A. machalana*, attacks cassava in Colombia, Venezuela, and Ecuador (Bellotti et al. 1999; Bellotti 2000b).

Vatiga illudens and V. manihotae. These two species attack cassava mainly during dry seasons, with attacks worsening in prolonged droughts. Adult *Vatiga* are gray and measure about 3 mm long and 1 mm wide. The average life cycle of *V. illudens* lasts 75.5 days. The female can lay, on average, 61.2 eggs, which she inserts into leaf tissue, preferably next to central nervures where they converge near the petiole. They thus become imperceptible. The nymph is white and a little smaller than the adult. Both adults and nymphs are found in large numbers on the underside of leaves.

Populations tend to concentrate on the basal and central leaves but, during severe attacks, may reach apical leaves. Damage caused in leaves is similar to that made by mites: small white spots of star-like appearance, giving a whitish appearance to the leaf as they join. They later acquire a reddish-brown tone (Bellotti 2000b). This damage differs from that made by mites by the presence of black points on the underside of leaves, which are excrements from the bugs. Foliage can be sufficiently damaged to extensively reduce photosynthesis and result in the defoliation of basal leaves (Bellotti 2000b).

Amblystira machalana. This pest induces a similar symptomatology to that induced by the *Vatiga* spp. Adults and nymphs of *A. machalana* appear black. The female lays, on average, 93 eggs on the underside of leaves. At first, they are white, but quickly become red or orange. The life cycle of *A. machalana* averages 42.5 days (Arias and Bellotti 2001). In the field germplasm bank held at CIAT, severe outbreaks of *A. machalana* have occurred during wet periods. This species is also found in subhumid zones of Ecuador (B Arias and JM Guerrero 1999, pers. comm.), unlike *V. illudens* and *V. manihoti*, which are more common in dry seasons.

In field trials at CIAT, natural populations of *A. machalana* led to yield losses of 39%, unlike for the plots of plants treated with pesticides (CIAT 1990). The literature contains little information on yield losses caused by *V. illudens* and *V. manihotae*. Populations of *V. illudens* in Brazil are endemic, and do appear to reduce yields, especially in the central Cerrados and, more recently, southern Brazil. Nor is much literature available on the current and potential damage of this pest, requiring more research (Bellotti 2000a, 2000b).

Controlling lace bugs. Control seems difficult, as they have very few natural enemies (Bellotti et al. 1999). Continuous use of insecticides is expensive and may destroy the natural enemies of other pests. Preliminary studies and evaluations made in the cassava germplasm bank held at CIAT indicate that varietal resistance may exist, but that more research is needed to develop the technology (CIAT 1990; Bellotti 2000a).

At CIAT–Palmira, a hemipteran of the family Reduviidae (*Zelus nugax*) was observed preying on the nymphs and adults of the *Vatiga* species mentioned above. It succeeded in consuming, throughout its biological cycle, an average of 475 lace bugs. Several spider species also feed on these insects but, so far, their potential as predators has not been measured.

Planthoppers

Thrips

Several thrips species have been identified as attacking cassava: *Frankliniella williamsi* Hood, *Scirtothrips manihoti*, *Corynothrips stenopterus*, and *Caliothrips masculinus*. All belong to the family Thripidae. Thrips are a pest in Central and South America, and have also been reported in Africa.

Frankliniella williamsi and Scirtothrips manihoti. These two species are the most important for the damage they cause to terminal buds in cassava plants, that is, they break the plants' apical dominance. The adult of both species is uniformly yellow, with microscopic differences.

When these thrips attack the plant, leaves do not develop normally; the folioles become deformed and present chlorotic yellow spots or small and irregular tears (in the sense of "rip"). The damage done by the thrips' scraping-sucking mouth apparatus to leaves-in-expansion causes them to deform to the point that complete leaf lobes are missing. New leaves are small with deep clefts that run from foliole margins to central nervures.

Brown lesions appear on stems and petioles, corresponding to scars, that is, to cork-like tissue that develop as wounds heal after the insects' scraping. Internodes are also shortened, and terminal growing points may die, inducing the growth of lateral buds, which then undergo attack from the pest. The result is a dwarf plant with a witches'-broom appearance. Thrips mostly attack in the dry seasons, with the affected plants recovering in the rainy season.

Corynothrips stenopterus and Caliothrips masculinus. These two thrips species are considered to be of lesser importance because they prefer the central and lower leaves of the plant. They do not break its apical dominance, thus enabling the plant to develop well. If attack is severe, leaf blades become full of small cork-like wounds that disfigure the plants' general aspect.

Corynothrips stenopterus is yellow with black spots in the last two abdominal segments. This coloring easily distinguishes the insect in the field. *Caliothrips masculinus* has a black body that generally measures 1.0 to 1.5 mm long and less than 1.0 mm wide. It is found on the expanded leaves of young plants, especially in greenhouses or screenhouses. It is rarely observed on field crops.

At CIAT, yield reductions from thrips attacks were studied. Results indicated that thrips can cause yield losses ranging from 15% to 20%, a finding that agrees with the literature. However, in highly susceptible varieties (e.g., 'Chiroza Gallinaza') growing in hot environments such as northern Cauca and Valle del Cauca, thrips attacks can prevent plant development, which, if compounded by weed invasion, will kill the plants (B Arias 1989, pers. comm.).

Some thrips species are fully developed within 15 to 30 days. They pass through four instars, two of which take place in the soil where they do not feed. In one year, they produce five to eight generations (Metcalf and Flint 1972, cited by Tejada 1975).

Control through varietal resistance. The best control method is to plant resistant varieties, which are readily available. Currently, more than 30% of the cassava varieties and hybrids carried by the germplasm bank held at CIAT are highly resistant to thrips attack, with a large percentage presenting symptom, that is, damage, of little consequence (CIAT 1974; Schoonhoven 1974; Arias and Guerrero 2000). Cassava resistance to thrips is based on the villosity of its leaf buds. If leaf pubescence is increased before they are expanded, then resistance to the thrips *F. williamsi* is increased. Such resistance is mechanical (Schoonhoven 1974; Arias and Guerrero 2000).

Cassava mealybugs

More than 15 mealybug species feed on cassava plants in Africa and South America. Species in the Americas include *Phenacoccus herreni*, *P. manihoti*, *P. madeirensis*, *Ferrisia virgata*, and *Pseudococcus mandioca* (Bellotti et al. 1983b; Williams and Granara de Willink 1992). *Phenacoccus herreni* and *P. manihoti* are of tropical origin and are economically important.

Phenacoccus manihoti was introduced into Africa in the early 1970s. The pest spread rapidly, causing considerable losses in crop yields. This motivated the development of a successful biological control program (Herren and Neuenschwander 1991). In the Americas, *P. manihoti* is found in Paraguay, certain areas of Bolivia, and the state of Mato Grosso in Brazil, where it is not economically significant (Lohr and Varela 1990). *Phenacoccus herreni* is dispersed throughout northern South America and Northeast Brazil, where high populations of the insect can cause considerable losses (Bellotti 2000a, 2000b).

Biology and behavior. Both species cause similar damage: feeding nymphs and adults causes leaf yellowing and curling, and a rosette formation in growing points. High populations cause tissue necrosis, defoliation, stem deformation, and bud death. Infested plants also suffer reduced rates of photosynthesis and transpiration, and loss of mesophyll efficiency. Moderate deficits of water pressure occur, and levels of internal CO_2 and leaf temperatures drop (CIAT 1992; Bellotti 2000a, 2000b).

Phenacoccus manihoti is parthenogenic. In contrast, males are needed for *P. herreni* to reproduce. On the underside of leaves and around apical buds, *P. herreni* females deposit ovisacs that contain several hundreds of eggs. The eggs hatch in 6 to 8 days and the insects undergo four nymphal instars, with the fourth instar being the adult. Males, however, have an extra instar. The third and fourth instars occur in a cocoon from which they emerge as winged adults.

Adult males live alone for 2 to 4 days. The female's average life cycle is 49.5 days, whereas that of the male is 29.5 days. The optimal temperature for female development is between 25 and 30 °C (Herrera et al. 1989; Bellotti 2000a, 2000b).

Phenacoccus herreni presents high population peaks during dry seasons. The beginning of the rains reduces these populations, allowing the crop to recover (Herrera et al. 1989). Recent research indicates that, when water supplies are limited, cassava leaves increase the concentrations of certain metabolites, which probably favor mealybug growth and reduce the effectiveness of parasitoids (CIAT 1999; Polanía et al. 1999; Calatayud et al. 2000). These results would help explain the rapid growth of mealybug populations during dry seasons (Bellotti 2000a, 2000b).

Control by varietal resistance. Identifying cassava resistance to the mealybug was hard, involving the evaluation of more than 3000 cultivars held in the germplasm bank at CIAT. Only low levels of resistance or tolerance were identified (Porter 1988). Studies on resistance made by IITA in Africa and by IRD have obtained similar results. Low to weak levels of resistance to *P. manihoti* have also been reported (Le Ru and Calatayud 1994; Neuenschwander 1994a). Such low levels of resistance may therefore require increased use of natural enemies in biological control programs (Bellotti 2000a).

Biological control. Mealybug management is a well-documented example of classical biological control, especially in Africa. *Phenacoccus manihoti* is now successfully controlled by the parasitoid *Apoanagyrus lopezi* after its introduction from the Neotropics. *Phenacoccus herreni* is distributed across northern South America, but only in Northeast Brazil does it cause severe yield losses. The mealybug may be exotic to that region, probably originating from northern South America (Williams and Granara de Willink 1992; Bellotti 2000a).

Numerous species of parasites, predators, and entomopathogens of *P. herreni* have been identified in the Neotropics. Many are generalist predators that feed on numerous species of mealybugs. However, several parasitoids prefer *P. herreni*, including those from northern South America:

Acerophagus coccois
Apoanagyrus diversicornis
Ap. elegeri
Anagyrus putonophilus
An. insolitus
Aenasius vexans

Three encyrtid parasitoids (*Ap. diversicornis, Ac. coccois*, and *Ae. vexans*) were found to be effective for controlling *P. herreni* (Van Driesche et al. 1988, 1990). *Aenasius vexans* and *Ap. diversicornis* noticeably prefer *P. herreni*, although laboratory studies indicate that they also parasitize other species of mealybugs (Bellotti et al. 1983b, 1994; Bertschy et al. 1997). The parasitoid *Ac. coccois* showed equal preference for either *P. herreni* or *P. madeirensis*. The three parasitoids are attracted by infestations of *P. herreni* (Bertschy et al. 1997). Comparative studies of the three parasitoids' life cycles show that each could complete two cycles for every cycle of *P. herreni*, a favorable ratio for biological control.

Apoanagyrus diversicornis prefers third-instar nymphs, while *Ac. coccois*, which is much smaller, parasitizes male cocoons, adult females, and second-instar nymphs with equal frequency. Oviposition of *Ap. diversicornis* caused a 13% mortality rate in third-instar nymphs (Van Driesche et al. 1990). *Aenasius vexans* prefers, with equal frequency, the second and third instars and adult females (CIAT 1990).

Field studies with natural populations of *Ap. diversicornis* and *Ac. coccois* revealed a percentage of parasitism when trap plants were established as hosts of *P. herreni* around the cassava crop (Van Driesche et al. 1988). The combined action of the two parasitoids caused a 55% mortality rate of *P. herreni* (Van Driesche et al. 1990).

Joint efforts by CIAT and EMBRAPA ensured that *Ap. diversicornis, Ac. coccois*, and *Ae. vexans* were exported from CIAT for release in Northeast Brazil, mainly in the states of Bahia and Pernambuco, between 1994 and 1996. Before this introduction, EMBRAPA scientists had conducted field studies to measure pest damage and collect natural enemies. At the end of 1996, more than 35,000 individuals of the three parasitoid species had been released. In Bahia, after release, *Ap. diversicornis* had dispersed up to 130 km in 6 months, 234 km in 14 months, and 304 km in 21 months.

In the same state, *Ac. coccois* also established and was recovered in large numbers at distances of less than 180 km from the release site 9 months later. *Aenasius vexans*, however, was continually recaptured in its site of release in Pernambuco, dispersing only

40 km in 5 months (Bento et al. 1999). Subsequently the authors observed that mealybug populations were noticeably reduced in that region and that the cassava crop was returning to areas that had been abandoned because of *P. herreni* infestations.

Stem-Perforating Insects

Shoot flies

Damage by shoot flies (*Silba pendula* and *Carpolonchaea chalybea*) is found in almost all cassava-producing regions of America. This pest has not been reported in either Africa or Asia.

Damage. Damage caused by larval shoot fly is manifested as a white exudate that flows from the growing point, which then usually dies. The exudates then change color from pale coffee to black as the latex oxidizes and dries up as the terminal point dies. Inside an attacked growing point, several larvae are found, which perforate the first 5 to 7 cm of the plant's terminal point tissue. Hence, the name "shoot fly".

Attacks by this pest delay plant growth and break its apical dominance. This stimulates the development of lateral buds, which may also suffer attack from this fly. Sometimes, only one part of the apical bud dies and the shoot continues growing. The youngest plants are the most susceptible, and repeated attacks may lead to plant dwarfism. In severe outbreaks of the pest, up to 86% of crop plants can be affected.

In studies simulating damage, between 50% and 100% of shoots were cut with a scalpel in each of two sets of plants, one aged 2–5 months, and the other 5–9 months. The late-branching variety M Ecu 150 was more susceptible than the 'Llanera' in the first 2 to 5 months of crop growth, with yields dropping by 30%. Removal of shoots from plants aged 6–9 months did not affect yield in any variety. Other trials in which damage was simulated (Arias and Bellotti 1982) indicated that root yield in variety M Col 22 was not reduced by shoot fly attack. However, an attack on a 3-month-old crop reduced optimal quality of planting stakes by 51% to 71%.

Biology and behavior. The adult fly is black with a metallic blue sheen. The female oviposits among leaves that have not, as yet, initiated expansion and in growing points, perforating a small cavity in the plant tissue with her ovipositor. Up to 22 eggs have been observed in one shoot, although the average is 3 to 8 eggs per shoot. The eggs are shaped like microscopic rice grains and hatch 4 days after oviposition. The young larvae then tunnel into the bud, impeding the meristematic leaves from opening. A milky discharge then appears and the growing point dies. Several whitish larvae can be observed inside the affected terminal point, where they live for about 23 days until they drop to the soil. They then pupate and, about 26 days later, the adult flies emerge. The flies are most active on sunny days, especially affecting cassava crops associated with banana or shade trees.

This pest attacks throughout the year, although, in many non-seasonal areas, they frequently appear at the beginning of the rainy season. At the CIAT–Palmira station, the dry climate favors the development of shoot-fly populations.

Trials that have confirmed a 100% loss of apical buds have not yet provided data on yield losses. Nor have the population dynamics of this pest been studied in detail. For these reasons, shoot fly is considered as a minor pest.

Control. Because this pest does not attack the whole crop and root production is not significantly reduced, the few apical buds found to be infested can be eliminated by hand, thus avoiding unnecessary applications of chemical products. However, when shoot-fly attack occurs early, affects all buds, or populations are high, application of an organophosphorus systemic insecticide is recommended. A mixture of insecticide and sugar solution sprayed onto plants forms an effective bait for controlling adults. Also recommended are traps containing decomposed fruits, casein, or yeast. These attract the insects, which can then be killed with insecticide.

Fruit fly

In Colombia and in America generally, two fruit fly species have been identified as attacking cassava: *Anastrepha manihoti* da Costa Lima and *A. pickeli* da Costa Lima (Diptera: Tephritidae). This observation is the first report of the pest attacking cassava fruit but does not cause significant economic losses. In Colombia, Venezuela, and Central America, fruit flies also cause severe damage to cassava stems.

Biology and behavior. The adult fly is yellowish coffee in color and about 10 mm long. It has transparent wings adorned with yellowish coffee-colored bands, which gives it a showy appearance. The female's abdomen presents a noticeable extension, corresponding to the ovipositor, whereas the abdomen in the male is rounder.

After oviposition, hatching takes place in the fruit. The larvae perforate and then destroy the developing seed. The infested fruit loses its green color, becomes soft, withers, and finally blackens (CIAT 1976). Damage to fruit is important to plant-breeding programs because seeds developed from crosses or hybridizations are then lost.

If it does not find cassava fruits, the female fruit fly seeks tender tissue on which to deposit her eggs. Such tissue is found in stems of young plants or in the terminal points of adult plants. The eggs are inserted into the tissue and can be recognized by the presence of a respiratory siphon, which looks like a small whitish eyelash that stands up from the stem tissue. Plant tissue around the eggs decomposes and becomes blackish. The whitish larvae that emerge from these eggs soon begin boring into the stems, moving either up or down and forming brown galleries in the stem's pith, which then begins to rot. Sometimes, the bud dies. When the larvae reach the prepupal state, they make orifices in the stems, which are then abandoned as the insects fall to pupate in the soil (Vidal and Marín 1974). Latex then oozes out of these orifices and drips down the length of the stems. The total life cycle of the fruit fly *A. pickeli* averages 39.5 days.

Damage. The damage caused by *Anastrepha* flies is associated with the rot caused by the bacterium *Erwinia carotovora* pv. *carotovora* (Mattos 1977). The bacterium penetrates the plant at oviposition or when the larvae leave to pupate. Other secondary pathogens are also found together with this bacterium.

The association between fruit fly and bacterium is not yet fully understood. Apparently, the bacterium is found on the stem where it lives as an epiphyte. However, it is most unlikely that the fly itself transports the bacterium. On the contrary, the bacterium penetrates the stems through the openings that the larvae have dug in stem tissues under conditions of high humidity. Under favorable conditions of precipitation and humidity, the stems rot (CIAT 1976). Stem rot does not favor larvae. When researchers examined rotten stems, they found that 40% of the larvae had died. Consequently, population increases of the insect may be attributed mostly to infestation of fruits of either cassava or other alternative hosts, and not so much to infestation of stems (Bellotti and Schoonhoven 1978c).

In affected stems, the rotting medulla region is either coffee-colored or brown, changing from pale to dark. Stakes obtained from these stems may lose as much as 16% of their capacity for shooting and may take several weeks to sprout.

Control. At crop establishment, stakes must be selected and only those that have healthy white piths should be planted. The most serious damage coincides with the rainy season, a time during which plants may recover rapidly and thus perhaps not need control measures.

The braconid *Opius* sp. parasitizes the larvae found in fruits by as much as 16%. However, it has not been found parasitizing larvae in stems.

Compared with other tried solutions, McPhail traps, which contain hydrolyzed maize at 2%, capture the most adult fruit flies from developing plants.

When adult populations are very high during the crop's first 3 to 4 months, chemical control may provide an alternative. Fenthion or dimethoate controls this pest well at doses between 2 and 3 mL of p.c. per liter of water. To avoid heavily contaminating the environment, chemical control should be carried out in that small area of the crop from which stakes will be obtained for the next cropping cycle.

Stemborers

The economically most important arthropod stemborers belong to the orders Coleoptera and Lepidoptera. They form a complex that feeds on cassava stems and branches, causing considerable damage to the crop, whether sporadically or locally, or mostly in adult plants. Although global in distribution, stemborers are much more important in the Neotropics, especially in the Latin American countries of Brazil, Colombia, and Venezuela. They tend to be highly specific to cassava, with only a few, reportedly, feeding on alternative hosts. None can be considered as a universal pest. They include the following species:

- The longhorned beetle (*Lagocheirus* spp.) is distributed throughout the entire world, but does not cause severe damage in the field.

- In Brazil, several species of *Coelosternus* (Coleoptera: Curculionidae) have been reported as reducing cassava yields and the quality of planting materials. Damage is usually sporadic and does not significantly affect yield (Bellotti and Schoonhoven 1978a, 1978b).

- Several lepidopterans and coleopterans attack cassava in Africa, with *Coelosternus manihoti* being considered a pest on that continent.

- Seven species of *Coelosternus* attack cassava in America.

The pests *Coelosternus* spp., *Lagocheirus araneiformis*, and *Chilomima clarkei* are presented below in more detail.

Coelosternus spp. This insect's larvae vary in size and form, according to species. Some measure as long as 30 mm. They are usually white, yellow, or cinnamon, and can be found tunneling into the plants' aerial parts. In susceptible varieties, the cassava plant's stems and branches may break or are reduced to sawdust. During dry seasons, the branches lose their leaves and may die. If infestation is severe, young plants may die. In infested branches, or on the soil below, waste matter and sawdust residues excreted or expelled by the larvae can be found.

The *Coelosternus* female may oviposit anywhere in the cassava plant, although it prefers the tender parts. For example, *C. alternans* oviposits near broken or cut extremes of branches or under the cortex in cavities perforated by the insect with its proboscis. Three days after mating, the *C. granicollis* female will penetrate the stem and oviposit white eggs.

When totally developed, *C. alternans* larvae measure 16 mm long and a maximum of 4 mm wide. Those of *C. tardipes* measure 9 × 2.5 mm. The white or reddish-brown bodies of most of these larvae curve. Their jaws are black. For *C. rugicollis*, only one larva is found per stem, whereas other species may have several larvae per stem. The larval phase lasts from 30 to 69 days. In all species, well-developed larvae pupate within cells they construct in the stem's pith. A pupa can hang within its own cell because one extreme is attached by substances excreted by the larva to the perforation made in the stem. The pupal phase lasts about 1 month.

The adult is a weevil, that is, it has a long proboscis. After emerging from the pupa, it remains in the cell for several days before abandoning the stem. Adults may be 6 (*C. granicollis*) to 12 mm long (*C. alternans* and *C. rugicollis*), and range from pale to dark brown, being almost totally covered with yellowish scales. Adults are active throughout the year, although less so at some sites during cool months.

Lagocheirus araneiformis. This insect (Coleoptera: Cerambycidae) has been found in a diversity of places such as the USA, Caribbean Region, Central and South America, the West Indies, and Indonesia. In Colombia, it is found in most cassava-growing regions and is believed to be the most abundant cerambycid in the country's cacao-growing areas (Villegas 1984). In addition to cacao (*Theobroma cacao*), other host plants include an ornamental plant known as tree spinach (*Cnidoscolus aconitifolius*).

<u>Biology and behavior</u>**.** The adult of this insect has antennae that are longer than its body. Its head, wide and grooved, stands out from between antennal tubercles, which are distant from each other. The *L. araneiformis* body is covered by short, light brown pubescence, with spots due to a darker or whitish pubescence. The elytra present rounded shoulders that darken at the base. Each elytron has two short spiny ribs. Two spots can also be seen on the elytra: one that is more or less triangular with its middle point at the base on the margin; and the other is lateral, darker, and located on each side close to where the elytron joins the body at the third pair of legs.

The female insect has an average body length of 1.64 cm and is 0.69 cm wide. The average male is similar, at 1.60 cm long by 0.72 cm wide. Mouth parts are used for masticating, and the antennae are filiform and light brown in color, and possess 11 segments. These also enable differentiation of sexes in both adults and pupae.

The adult female oviposits in stems and branches at about 2.5 mm below the cortex. She first uses her jaws to open a small perforation with a diameter of about 0.72 mm in the cortex of buds and internodes. She then deposits her egg in either a horizontal or oblique position. The postures adopted are individual and, occasionally, two eggs are placed at an average depth of 1.02 mm. The preoviposition period is usually 9.7 days and that of oviposition is 28.8 days (ranging from 13 to 62). During the latter period, the female lays an average of 150 eggs (ranging from 87 to 202). She prefers to oviposit at night, although 10.2% of eggs are laid during the day (Villegas 1984).

A newly laid egg of *L. araneiformis* is whitish cream, turning yellow by the second day. Close to hatching, one extreme shows a dark coffee-colored spot, which corresponds to the larva's jaws. The egg is elliptical, of hard consistency, and measures 0.76 mm at its equatorial and 2.04 mm at its polar diameters. Incubation takes an average of 3.13 days (ranging from 2 to 6 days).

The larva is apodal, cream in color, and, because of its shape, is often known as *gusano tornillo* in Spanish. The name comes from its compressed and prognathic head, which is adhered to a very wide prothorax that gives the insect a cylindrical appearance. This feature is carried to adulthood, giving rise to its name as *flat-faced longicorn beetle*. The head is dark brown, chitinized, and carries strong jaws. Dorsally, the thorax presents two, chitinized, light brown plates. The abdomen has 10 well-defined segments, with the last one being rounded and smaller. The larva measures 0.3 mm in the first instar, growing to 37 mm by the sixth instar.

Pupae are exarate. When recently formed, pupae are light brown, becoming darker as they develop. When an adult is close to emerging, its sex can be differentiated by its antennae. The male also exhibits, between the fourth and fifth joints, a wisp of hair that is not found in the female, who, in contrast, has two pairs of spinules in the last abdominal segment.

In the field, the life cycle of *L. araneiformis* lasts 86 to 194 days, with an average of 128.2 days. Adult females live an average of 89.7 days and males 91.6 days. In the laboratory, these periods were shorter, at 45.8 and 71.8 days, respectively (Villegas 1984).

Damage. The larvae of *L. araneiformis* move within the stem by using their jaws and contracting their bodies. Recently hatched larvae are located in the cortex on which they feed during the first instar. Second instars partially consume the cortex but also open galleries to tissues lying nearest to the ligneous area, where they begin the third instar. They continue to bore through the stake or stem to its central parts, where the last instars and pupae develop, thus completing their life cycle.

In the field, the pest attacks both recently planted stakes and already developed plants. They also attack planting materials that have been stored for long periods. When recently planted stakes are attacked, the seedlings die or they suffer poor sprouting. In contrast, when already developed plants are attacked, damage is local, usually at the base of the stem, which may provoke lodging if the attack is severe. In plants that have fallen, up to 30 larvae per plant have been found. Larvae also attack roots, forming galleries through which microorganisms can penetrate to cause secondary rots that reduce yields. Plants attacked by *L. araneiformis* are easily recognized in the field by the presence of light brown or reddish brown sawdust, of rough texture, that larvae expel as they bore through stems.

Control. Chemical control of this and all stemborers is difficult. The following farming practices are therefore recommended:

- Harvest residues, which help disseminate the insect, should be collected and burned.
- Biological control of this insect has not yet been found. Hence, one method for regulating adult populations is to place traps made of packages of fresh stakes in the field, thus attracting them and enabling their capture.
- Careful selection of planting stakes.

Chilomima clarkei. This stemborer (Lepidoptera: Pyralidae) is a butterfly whose larvae bore or perforate cassava stems. Recently, this insect has greatly increased its populations in Colombia and Venezuela to become, currently, the most important cassava pest (López et al. 1996). The pest causes root production losses of more than 60% because the stems break, debilitated by the attacks. In Colombia, in the late 1990s, *C. clarkei* became the most important pest in several departments of the Atlantic Coast, destroying planting materials to the point of causing a crisis. The pest disseminated very rapidly through the exchange of stakes from region to region among farmers (B Arias 1985, pers. comm.). In the Colombian Caribbean Region, 85% of planted cassava is attacked by *C. clarkei* (López et al. 1996).

This pest has also been found in Tolima, Huila, Caldas, the two Santanders, the Eastern Plains of Colombia, and the Western Plains of Venezuela. It has also been reported in other countries such as Argentina and Brazil (A Bellotti 1985, pers. comm.). To date, the pest has not been reported in environments at altitudes of more than 400 to 500 m above sea level. It is very important, therefore, that planting materials from these sites are not transported to areas where the pest does not exist, without the necessary precautions being taken or without phytosanitary certification.

Females are nocturnal in habit, and live for 5 to 6 days (males for 4 to 5 days). Oviposition takes place at night on cassava stems, usually near a node or bud, with females laying an average of 229 eggs. The eggs are very small and flat, and difficult to see in the field, as they measure less than 1 mm in diameter. They are laid either individually or in small groups of 2 to 5. They are at first cream in color and, as they mature, take on a pink tinge. The eggs hatch about 6 days later (at 28 °C).

Damage. After hatching, the first-instar larvae feed on the stem cortex or epidermis. These larvae are very mobile, seeking appropriate sites at which to feed, almost always near axillary buds. They form a capsule for protection, living and feeding within it until they reach fourth instar. At each instar, the capsule's tissues stretch. A fine and abundant sawdust can then be observed, unlike for *L. araneiformis*. During fifth instar, the larvae penetrate the stems where they complete the next 6 to 12 instars, pupate, and then emerge as adults (Lohr 1983). The larval states take 32 to 64 days to complete and the pupal state 12 to 17 days.

Populations of *C. clarkei* may be present throughout the year and increase during rainy seasons. Four to six cycles of the pest may occur during a cropping year, potentially increasing damage and making control much more difficult. When the number of perforations made in the stem is already considerable (e.g., more than 20 per stem), the stem could break, reducing the quality and quantity of planting materials. In the field, plants with more than 35% of stem parts under attack suffer significant reductions (45% to 62%) in root yields (Lohr 1983).

Control by host-plant resistance. Once the larvae enter the stems, control is very difficult. The capsules woven by the larvae for protection against natural enemies also protects against pesticides. However, the great mobility of first-instar larvae makes them highly vulnerable, which means they can be controlled by entomopathogens such as *Bacillus thuringiensis*. Given the pest's generational increase, several applications will be needed, increasing production costs. Field research conducted by Gold et al. (1990) indicated that intercropping with maize reduces stemborer populations until the maize is harvested.

In Pivijay, Department of Magdalena, nearly 2000 cultivars held in the germplasm bank at CIAT were evaluated during 2 years for varietal resistance to this pest. Significant differences were found among the varieties, where some presented 20 to 30 holes, with a maximum of 70, in six plants; and others an average of one hole per plant, also in six plants. CIAT will continue to assess varieties to tackle the pest through cassava plant resistance.

Biological control. Several biological control agents have also been identified as attacking both eggs and larvae of *Chilomima* sp. Eggs are parasitized by *Trichogramma* microhymenopterans; and larvae by *Bracon* wasps, *Brachymeria conica*, and *Apanteles* sp. (Lohr 1983).

Known control methods were evaluated in the 1980s when research on the pest started. Applications of *Bacillus thuringiensis,* the fungus *Spicaria* sp., and macerated larvae that had died from a probable viral disease were each sprayed over pest larvae, resulting in a mortality rate of 99%, 88%, and 100%, respectively (Herrera 1999). The great mobility of first instars made them much more vulnerable to several products, to the point where they could be controlled with *B. thuringiensis*.

CIAT initiated research to introduce resistance genes to insects, using *B. thuringiensis* through the vector *Agrobacterium* to transform embryonic tissues of cassava, thereby developing cultivars resistant to *C. clarkei*. Initial results are so far promising (CIAT 1999).

Other controls. As mentioned previously, control with insecticides is not practical because adult stemborers are difficult to kill and their larvae feed inside stems. Farming practices that reduce this pest's populations include the removal and burning of infested plant parts and the planting of healthy undamaged stakes (Bellotti et al. 1983a). Other useful practices are to treat the stakes, burn harvest residues, store stakes for short periods, and avoid exchanging stakes between sites. Technical personnel and farmers must also be trained to manage the pest and disseminate the message of how important such management is.

Technicians working in the Colombian Atlantic Coast have evaluated the local use of insecticides to manage *Chilomima* attacks. Among the several pesticides they evaluated, they found that malathion, applied manually with "polyspray" in doses ranging from 0.5 to 1.0 p.c. per liter of water and directly into holes containing sawdust, resulted in 100% larval mortality over time and even prevented the pest's dissemination in the locality (E Ortega 2001, pers. comm.). The practice is interesting because the applications were not generalized but made specifically at the points, thus favoring both beneficial fauna and the environment. Furthermore, applications were easy to do, although workers must be duly protected.

Cassava burrower bug

Cyrtomenus bergi Froeschner is an arthropod pest that feeds directly from cassava roots. The species is polyphagous and so had not coevolved with the crop. García and Bellotti (1980) first reported this pest attacking cassava in Colombia in 1980.

Distribution and behavior. Recently, the pest was reported as causing commercial damage in Panama, Costa Rica, and Venezuela (Riis 1997). The insect is present in many other Neotropical regions, where it has been found feeding on many crops, including onion, groundnut, maize, potato, *Arachis pintoi* (forage groundnut), sorghum, sugarcane, coffee, coriander, asparagus, beans, peas, some grasses, and several weeds (Riis 1997; Bellotti et al. 1999; Bellotti 2000a, 2000b).

The pest prefers certain host plants to others. Free-choice feeding tests conducted in the laboratory indicated that cassava is not the optimal host. The bug prefers groundnut or maize to cassava (78% vs 22%), growing much faster in maize. The adult life span in maize was 95 days, 69 in onion, 66 in sweet cassava (CMC 40), and 64 days in bitter cassava (M Col 1684) (Riis 1990). Optimal fecundity, survival rate, and intrinsic rate of increase in the population were recorded in groundnut and *Arachis pintoi* but not in maize. Sweet cassava, sorghum, and onion were the least favored hosts. It could not complete its life cycle in bitter cassava varieties (Riis 1997; Bellotti 2000a, 2000b).

Damage. Nymphs and adults of *C. bergi* feed on cassava roots, penetrating the peel and parenchyma with their thin and strong stylets. This feeding action enables several soil pathogens (e.g., fungal species of *Aspergillus, Diplodia, Fusarium, Phytophthora*, and *Pythium*, and the alga *Genicularia* sp.) to enter the root parenchyma (Arias and Bellotti 1985a; Bellotti and Riis 1994) and cause coffee-colored to black lesions that give the insect the Spanish name of *chinche de la viruela* or, literally, "smallpox bug". Lesions begin appearing in roots 24 h after feeding (Arias and Bellotti 1985a). They may lead to reduced starch contents and hence to serious losses in the roots' commercial value. Damage is not detected until the roots are harvested and peeled. Consequently, farmers lose the investment they made in cultivation tasks, time, and use of land.

Populations of *C. bergi* are present in the soil throughout the cropping cycle and damage to roots can be seen within the crop's first month. At the end of the cycle, the bugs may have damaged, through their feeding action, between 70% and 80% of all roots, reducing starch content by more than 50%. Serious economic damage is not necessarily caused by large *C. bergi* populations (Arias and Bellotti 1985a). Riis (1990) showed that, even with very small populations (close to zero), 22% of roots can be affected. The economic threshold, where a cassava buyer would reject a load of roots, is damaged parenchyma in 20% to 30% of roots, that is, when they present "cosmetic" damage due to the dark bite points, which are not acceptable to fresh-cassava markets (Bellotti 2000a, 2000b).

Life cycle. *Cyrtomenus bergi* presents five nymphal instars. The nymphs and adults may live for more than 1 year, feeding on cassava roots (García and Bellotti 1980). In the laboratory, at 23 °C and 65% ± 5% rh, when *C. bergi* was fed slices of cassava root with low levels of cyanide (HCN), its life cycle was 286 to 523 days. On average, eggs took 13.5 days to hatch, the five nymphal states 111.3 days to develop, and the adult life span was 293.4 days.

This bug is strongly attracted to moist soils. It will accordingly migrate when soil moisture content is less than 22% and will remain in soil that has more than 31%. The rainy season therefore enormously favors the survival of adults and nymphs and, thus, their behavior and dispersion. In contrast, low soil moisture content during dry periods will restrict the adults from hiding and migrating, and will increase nymph mortality (Riis 1997; Bellotti 2000a, 2000b).

Effects of cyanogenic glycosides. Field trials and laboratory studies suggest that *C. bergi* feeding preferences may be related to the levels of cyanogenic glycosides in cassava roots, as follows:

- Adults and nymphs that feed on a variety with high HCN content (i.e., more than 100 mg of cyanide [CN^-] per kilogram of roots) experience longer nymphal development, reduced egg production, and increased mortality.

- Oviposition on CMC 40 (43 mg CN^-/kg roots) was 51 eggs per female, compared with only 1.3 eggs on M Col 1684 (627 mg CN^-/kg roots).

- Adult life span on CMC 40 was 235 days, that is, more than double than that on M Col 1684 (112 days) (Bellotti and Riis 1994).

- Riis (1997) demonstrated that oviposition on clones with a cyanogenic potential (CNP) of less than 45 ppm fw was significantly higher than on clones with a CNP of more than 150 ppm. However, the rate changed considerably for clones where the CNP ranged between 45 and 150 ppm.

- Other studies have indicated that early instars are more susceptible than late instars to the roots' CNP. Indeed, the length of the bug's stylet during the first two nymphal instars probably restricts the insect's feeding action mainly to the root peel (Riis 1990; Riis et al. 1995), whereas the third to fifth instars can feed directly from the parenchyma. In cv. CMC 40, cyanogen levels in root parenchyma are low, but high in the peel at 707 mg CN/kg roots. Laboratory experiments in which the bug was fed CMC 40 resulted in a 51% mortality of first- and second-instar nymphs. This rate is high, even when compared with the 82% mortality of similar nymphs fed M Col 1684. Consequently, the high level of cyanogens in the CMC 40 cortex may be responsible for the insect's high mortality (Bellotti and Riis 1994; Bellotti 2000a).

- Studies of preferential feeding conducted in cassava fields in Colombia indicated that the level of damage was considerably higher for CMC 40 (low cyanogen contents) than for M Col 1684. Clone M Mex 59, whose cyanogen content is intermediate at 106 mg CN^-/kg roots, suffered moderate damage (Arias and Bellotti 1985a).

These data indicate that the CNP can impede *C. bergi* survival and that any damage caused should not be a problem when clones with a high CNP value are cultivated (e.g., in Northeast Brazil and Africa) (Bellotti and Riis 1994; Bellotti 2000a).

Control. Controlling *C. bergi* is difficult because of its polyphagous habits and adaptation to soil environments. Measures must be adopted in the crop's initial stages, either at planting or in the first 2 months, when initial damage may occur. The application of a pesticide may reduce pest populations and, thus, the damage. However, frequent applications would be necessary; these would be expensive, environmentally dangerous, and with no guarantee that the economic threshold of loss would be reduced (Castaño et al. 1985).

In cassava crops intercalated with *Crotalaria* sp., damage to roots was reduced to less than 4%, as opposed to monoculture where damage was 61%. However, yields of intercalated cassava were reduced by 22%. Unfortunately, *Crotalaria* sp. has little commercial value and farmers therefore refuse to adopt this technology.

Experimental data and field studies show that varieties with high CNP values are resistant to *C. bergi* attack and the damage it does. However, in many cassava-producing regions, sweet varieties (or those with low CNP) are preferred for fresh consumption. Recent studies indicate that potential for resistance or tolerance of *C. bergi* exists in 15 varieties with low CNP (Riis 1997). To take advantage of this varietal resistance, research needs to be carried out on the pest's behavior and the plant's mechanisms of resistance, both biochemical and genetic.

The potential for biological control of *C. bergi* is being researched. Recent studies with entomopathogenic nematodes and fungal pathogens indicate that they could be used for control. This research has, so far, been conducted only in the laboratory and greenhouse. Field studies must be carried out before the most acceptable technology can be recommended. Promising technologies include:

- The nematode *Steinernema carpocapsae*, which has successfully parasitized *C. bergi* in the laboratory. Infection was established within 5 to 8 days after exposure to the insect. The adult was the most sensitive to infection (58.6% parasitized after 10 days). The least susceptible were the first and second instars, with 17% and 31% parasitized, respectively (Caicedo and Bellotti 1994).

- A native nematode, *Heterorhabditis bacteriophora,* found as a field parasite in Colombia, had an average rate of parasitism at 84% on all instars of the pest (Barberena and Bellotti 1998).

- Isolates of the fungal entomopathogen *Metarhizium anisopliae* parasitizing *C. bergi* were collected in the field. Laboratory studies verified that the mortality rate is 61% for fifth instars, which is much higher than the overall average mortality rate at 33% (CIAT 1994).

Insects that Attack Stems Externally

Scale insects

In most cassava-producing regions, the following species of scale insects have been identified: *Aonidomytilus albus* Cockerell, *Saissetia miranda* Cockerell et Parrott, *Hemiberlesia diffinis* (Newstead), and *Ceroplastes* sp. Scale insects stay on stem surfaces, mostly close to buds, on which they feed. As their reproduction rate increases, the more they invade the stems.

These insects belong to the order Hemiptera, suborder Homoptera, superfamily Coccoidea, family Diaspididae. *Aonidomytilus albus* is commonly known as the white mussel scale, cassava scale, or tapioca scale. Economically, it is considered a major stem-sucking pest.

The family Diaspididae, the largest of the Coccoidea, includes protected scales, which themselves include the different scales that attack cassava. The name "scale" comes from the dense waxy secretion that the adult secretes, adding to the exuviae of the insect's first two nymphal states.

Damage. When a stem is invaded by scale insects, the leaves become yellow and fall. If the attack is severe, plant growth is retarded, stems dry up, and the plant dies. Such damage occurs especially when the attack is early, that is, when the plant is 2 to 3 months old. A generalized attack of scale early in the cropping cycle will seriously affect yields. Attacks occur especially during dry seasons. The greatest damage that scale insects cause is, apparently, the loss of planting materials. Heavily infested stakes produce few shoots (i.e., a low rate of germination), with a resultant deficient development of unpleasant-eating roots. The adult *A. albus* is shaped like a mussel and is covered with a waxy white secretion.

Life cycle. Swaine (1950) studied the biology of *A. albus* in detail. The molted exoskeletons (also called *exuviae*) of the first and second nymphal states are incorporated into the scale. Unlike the females, males have well-developed legs and wings. The female produces, on average, 47 eggs that are oviposited between the upper cover of the scale and the lower cottony secretion. During oviposition, the female drops in size. Eggs hatch 4 days later.

The first nymphal states are mobile and can disperse. One to four days later they become fixed and covered with numerous fine threads. After 11 days, they molt and become immobile. After 4 days, the adult female begins ovipositing 1 to 2 days later. A generation lasts 22 to 25 days.

Scale insects are dispersed by wind, by moving around on the soil, or through infested stakes. The environment in which scale insects spread most readily is the area where stakes are stored, when infested stakes come into contact with healthy ones.

Control. Two highly effective farming practices control scale insects: planting stakes that are not infested and burning infested plants to prevent dissemination. Biological control agents include the following:

- *Chilocorus distigma* (Coccinellidae), preys on *A. albus*.
- In Cuba, two hymenopterans have been reported (Aphelinidae) as parasitizing *A. albus*: *Aspidiophagus citrinus* and *Signiphora* sp. A brown, sponge-like fungus (*Septobasidium* sp.) was also found attacking *A. albus*.
- In Colombia, *Saissetia miranda* was found being parasitized by two microhymenopterans—*Anagyrus* sp. and *Scutellista* sp.—at a level of more than 79%.

Gall fly

In the Americas, several species of gall fly have been reported on the cassava crop, the most frequent of which is *Jatrophobia brasiliensis* Rubs. (Diptera: Cecidomyiidae). This small fly is usually found on the underside of leaves, where it lays its eggs. The tiny larvae leave the egg and penetrate the leaf mesophyll, provoking a defense reaction that is manifested as an abnormal growth (hypergrowth) of the leaf cells, giving its name *cassava leaf gall*.

Leaf galls are found on the upper leaf surface. They range in color from yellow to red, depending on the cassava variety, and are narrower at the base and are often curved. They measure up to 1 cm long and 0.5 mm wide. When a gall is opened, a cylindrical tunnel, containing a small yellow larva, is found. At the base of the gall, on the underside, the tunnel is connected to a small hole from which the adult emerges.

The gall fly is believed to have little economic importance and that it usually does not need to be controlled. In some regions of Colombia and Venezuela, galls are found almost as clusters on certain leaves and, in isolated cases, small plants are heavily attacked. To reduce a population of this fly, collecting and destroying affected leaves at weekly intervals is recommended.

Pests of Dried Stored Cassava

Storage of dried cassava started in Colombia in 1981 when a project of natural cassava drying was established in the country's Atlantic Coastal Region. Before then, farmers handled a highly perishable product that, after 2 days, was no longer adequate for human consumption or animal feed. In contrast, dried cassava provides a more stable product (Román 1983). However, storage conditions sometimes permit flour and dried cassava pieces and chips to deteriorate through the action of biological factors, including insect attack (Piedrahíta 1986). Pests of stored dried cassava not only reduce their quality but also consume significant quantities of this product.

Damaging species

Two principal species infest cassava chips: *Rhyzopertha dominica* and *Lasioderma serricorne*. They infest cassava during sun-drying. After 2 months of storage, the total weight of stored pieces may drop by as much as 16% (Motta 1994). Parker and Booth (1979) reported that, in Malaysia, the most abundant insects in a trial on stored dried cassava pieces were *Sitophilus zeamais*, *Cryptolestes klapperichi*, *Rhyzopertha dominica*, *Tribolium castaneum*, *Stegobium paniceum*, *Dinoderus minutus*, and *Latheticus oryzae*. For the most part, damage occurred to dried cassava imported from Asia or Africa.

CIAT scientists (CIAT 1983a) reported 38 insect species, mainly Coleoptera, in cassava flakes or other dried products. Many were polyphagous. In cassava flour, four species were found: *Tribolium castaneum, Lasioderma serricorne, T. confusum*, and *Rhyzopertha dominica*. In cassava pieces, three species were found: *T. castaneum, Araecerus fasciculatus*, and *L. serricorne*.

Tribolium castaneum H.

At CIAT, scientists studied *T. castaneum* H, also known as the red cassava weevil, which often causes serious damage, both as larvae and as adults. This pest enables other species to degrade stored dried cassava even further, causing losses in weight and quality.

Biological cycle. The total duration of the life cycle is 67.6 days at 25 °C and 56.6 days at 30 °C. At 20 °C, the larva does not completely develop. The egg incubates for an average 3.4 and 14 days, respectively, for the same temperatures. The average oviposition period for a group of five females was 60, 95, and 104 days at temperatures of 20, 25, and 30 °C, respectively. The average numbers of fertile eggs at temperatures of 20, 25, and 30 °C were, respectively 70, 217, and 214. The rate of oviposition per female was 0.16, 0.39, and 0.44 eggs per day, at the same respective temperatures (Motta 1994).

Damage. The red weevil feeds on cassava dried pieces, turning them into powder and so causing economic losses. It also infests flour, with losses being more moderate than for dried pieces. However, product contamination is inevitable, degrading product quality.

- In flour, an initial infestation of 50 adult insects per kilogram resulted in losses that ranged between 0.212% at 20 days and 0.875% at 90 days.

- In dried pieces, an initial infestation of 70 adult insects per kilogram resulted in losses that ranged between 0.462% at 30 days and 3.1% at 90 days (Motta 1994).

Evaluations of the type of packaging used to store dried cassava pieces and cassava flour have given interesting results: for example, polyethylene bags better preserve the quality of both pieces and flour than cloth bags or sisal sacks.

Control and management. Practices that control dried-cassava pests are the same as those applied to pests of stored grains. In both cases, the pests are the same and storage is usually under the same conditions.

The most effective measures for sanitary control are to clean and disinfect the storerooms before storage, rapid removal of infested material, and as short a storage as possible, preferably less than 3 months.

Bitter cassava varieties are more resistant than sweet varieties to these weevils, although this observation has yet to be confirmed. Fumigation is also effective for controlling these pests, provided that all the safety standards are met to guarantee success of the control operation.

Integrated System of Pest Control

Cassava is an ideal crop for developing a program of biological pest control because its vegetative phase (from 8 to 14 months) is long. The basic principles of such a program include:

- Ready availability of some resistance to pests, although high levels of resistance are not required.
- Inclusion of the insect–plant–environment interaction, as rainfall appears to be a key factor.
- Availability of agronomic practices (e.g., selection of planting materials and crop rotation) that will reduce pest incidence.
- Rational use of insecticides, only when strictly necessary.
- Avoidance of indiscriminate use of insecticides to prevent their interrupting established biological control programs.

Researchers are firmly convinced that a program of integrated pest management for the cassava crop should be supported by three actions: biological control, varietal resistance, and farming practices. Each will play an important role in the future.

References

The following acronyms are used to save space:

CIAT = Centro Internacional de Agricultura Tropical
SOCOLEN = Sociedad Colombiana de Entomología

Allem AC. 1994. The origin of *Manihot esculenta* Crantz (Euphorbiaceae). Genet Resour Crop Evol 41(3):133–150.

Angel JC; Pineda BL; Nolt B; Velasco AC. 1990. Moscas blancas (Homoptera: Aleyrodidae) asociadas a transmisión de virus en yuca. Fitopatol Colomb 13:65–71.

Arias B. 1995. Estudio sobre el comportamiento de la “mosca blanca” *Aleurotrachelus socialis* Bondar (Homoptera: Aleyrodidae) en diferentes genotipos de yuca, *Manihot esculenta* Crantz. MSc thesis. Universidad Nacional de Colombia–Palmira, Colombia. 181 p.

Arias B; Bellotti AC. 1977. Eficiencia de *Bacillus thuringiensis* sobre el gusano cachón de la yuca (*E. ello*), en un programa de control biológico. Rev Colomb Entomol 3(3/4):93–97.

Arias B; Bellotti AC. 1982. Daño simulado de la mosca del cogollo, *Silba pendula* Bezzi (Diptera: Loncheidae), en yuca (*Manihot esculenta* Crantz). In: Abstracts [of the] Proc IX Congress of SOCOLEN, Cali, Colombia. SOCOLEN, Bogotá, DC, Colombia. 9 p.

Arias B; Bellotti AC. 1983. *Phoenicoprocta sanguinea* (Lepidoptera: Ctenuchidae): Ciclo de vida y enemigos naturales. In: Abstracts [of the] Proc X Congress of SOCOLEN, Cali, Colombia. SOCOLEN, Bogotá, DC, Colombia.

Arias B; Bellotti AC. 1985a. Aspectos ecológicos y de manejo de *Cyrtomenus bergi* Froeschner, chinche de la viruela en el cultivo de la yuca (*Manihot esculenta* Crantz). Rev Colomb Entomol 11(2):42–46.

Arias B; Bellotti AC. 1985b. Ciclo biológico de *Erinnyis ello* (gusano cachón de la yuca) a diferentes temperaturas. In: Abstracts [of the] Proc VI Congress of SOCOLEN, Manizales, Colombia. SOCOLEN, Bogotá, DC, Colombia.

Arias B; Bellotti AC. 2001. Ciclo biológico, comportamiento e importancia económica de *Amblystira machalana* Drake (Hemiptera: Tingidae), la chinche negra de encaje, en el cultivo de la yuca. In: Abstracts [of the] Proc XXVIII Congress of SOCOLEN. SOCOLEN, Bogotá, DC, Colombia.

Arias B; Guerrero JM. 2000. Control de plagas de la yuca (*Manihot esculenta* Crantz) por resistencia varietal. In: Symposium on “Avances en el Manejo de Plagas”. Proc XXVII Congress of SOCOLEN, Medellín, Colombia, July 2000. SOCOLEN, Bogotá, DC, Colombia. p 243–259.

Barberena MF; Bellotti AC. 1998. Parasitismo de dos razas del nemátodo *Heterorhabditis bacteriophora* sobre la chinche *Cyrtomenus bergi* (Hemiptera: Cydnidae) en el laboratorio. Rev Colomb Entomol 24(1/2):7–11.

Bellotti AC. 2000a. El manejo integrado de las principales plagas de la yuca (*Manihot esculenta* Crantz). In: Proc. Primer Curso-Taller Internacional sobre Control Biológico, held at the Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Palmira, Valle, Colombia. Produmedios, Bogotá, DC, Colombia. p 210–243.

Bellotti AC. 2000b. Las plagas principales del cultivo de la yuca: Un panorama global. In: Symposium on "Avances en el Manejo de Plagas". Proc XXVII Congress of SOCOLEN, Medellín, Colombia, July 2000. SOCOLEN, Bogotá, DC, Colombia. p 189–217.

Bellotti AC; Arias B. 1988. Manejo integrado de *Erinnyis ello* (L.). CIAT, Cali, Colombia. 24 p.

Bellotti AC; Riis L. 1994. Cassava cyanogenic potential and resistance to pests and diseases. Acta Hortic 375:141–151.

Bellotti AC; Schoonhoven A van. 1978a. Cassava pests and their control. CIAT, Cali, Colombia. 71 p.

Bellotti AC; Schoonhoven A van. 1978b. Mite and insect pests of cassava. Annu Rev Entomol 23(1):39–67.

Bellotti AC; Schoonhoven A van. 1978c. Plagas de la yuca y su control. CIAT, Cali, Colombia. 71 p.

Bellotti AC; Reyes Q JA; Arias V B. 1983a. Manejo de plagas en yuca. In: Reyes JA, ed. Yuca: Control integrado de plagas. CIAT, Cali, Colombia. p 265–281.

Bellotti AC; Reyes JA; Varela AM. 1983b. Observaciones de los piojos harinosos de la yuca en las Américas; Su biología, ecología y enemigos naturales. In: Reyes JA, ed. Yuca: Control integrado de plagas. CIAT, Cali, Colombia. p 313–339.

Bellotti AC; Vargas H, O; Peña JE; Arias V, B. [1983c]. Pérdidas en rendimiento en yuca causadas por insectos y ácaros. In: Domínguez CE, ed. Yuca: Investigación, producción y utilización. CIAT; United Nations Development Programme (PNUD), Cali, Colombia. p 393–408.

Bellotti AC; Mesa N; Serrano M; Guerrero JM; Herrera CJ. 1987. Taxonomic inventory and survey activities for natural enemies of cassava green mites in the Americas. Insect Sci Appl 8(4/5/6):845–849.

Bellotti AC; Arias B; Guzmán OL. 1992. Biological control of the cassava hornworm *Erinnyis ello* (Lepidoptera: Sphingidae). Fla Entomol 75:506–515.

Bellotti AC; Braun AR; Arias B; Castillo JA; Guerrero JM. 1994. Origin and management of Neotropical cassava arthropod pests. Afr Crop Sci J 2(4):407–417.

Bellotti AC; Smith L; Lapointe SL. 1999. Recent advances in cassava pest management. Annu Rev Entomol 44:343–370.

Bento JMS; Bellotti AC; Castillo JA; de Morães, GJ; Lapointe SL; Warumby JF. 1999. Introduction of parasitoids for control of cassava mealybugs in northeastern Brazil. Bull Entomol Res 89(5):403–410.

Bertschy C; Turlings TCL; Bellotti AC; Dorn S. 1997. Chemically-mediated attraction of three parasitoid species to mealybug-infested cassava leaves. Fla Entomol 80(3):383–395.

Blair MW; Fregene MA; Beebe SE; Ceballos H. 2007. Marker-assisted selection in common beans and cassava. In: Guimarães EP; Ruane J; Scherf BD; Sonnino A; Dargie JD, eds. Marker-assisted selection: current status and future perspectives in crops, livestock, forestry and fish. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy. p 81–115.

Bohórquez C, A. 2011. Aislamiento de secuencias expresadas diferencialmente durante la respuesta de defensa al ataque de la mosca blanca (*Aleurotrachelus socialis*) en el cultivo de yuca (*Manihot esculenta* Crantz) mediante genómica funcional. Dissertation. Universidad Nacional de Colombia-Palmira, Colombia.

Braun AR; Bellotti AC; Guerrero JM; Wilson LT. 1989. Effect of predator exclusion on cassava infested with tetranychid mites (Acari: Tetranychidae). Environ Entomol 18(4):711–714.

Braun AR; Bellotti AC; Lozano JC. 1993. Implementation of IPM for small-scale cassava farmers. In: Altieri MA, ed. Crop protection strategies for subsistence farmers, Westview, Boulder, CO, USA. p 103–115.

Byrne DH; Guerrero JM; Bellotti AC; Gracen VE. 1982. Yield and plant growth responses of *Mononychellus* mite resistant and susceptible cassava cultivars under protected vs. infested conditions. Crop Sci 22(5–6):486–550.

Byrne DH; Bellotti AC; Guerrero JM. 1983. The cassava mites. Trop Pest Manage 29(4):378–394.

Caicedo AM; Bellotti AC. 1994. Evaluación Del potencial del nemátodo entomógeno *Steinernema carpocapsae* Weiser (Rhabditida: Steinernematidae) para el control de *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae) en condiciones de laboratorio. Rev Colomb Entomol 20(4):241–246.

Castaño O; Bellotti AC; Vargas O. 1985. Efecto del HCN y de cultivos intercalados sobre daño causado por la chinche de la viruela *Cyrtomenus bergi* Froeschner al cultivo de la yuca. Rev Colomb Entomol 11(2):24–26.

Castillo J. 1996. Moscas blancas (Homoptera: Aleyrodidae) y sus enemigos naturales sobre cultivos de yuca (*Manihot esculenta* Crantz) en Colombia. MSc thesis. Universidad del Valle, Cali, Colombia. 173 p.

CGP. 2009. Cassava Genome Project. Available at http://www.phytozome.net/cassava

CIAT. 1974. Informe anual [del] Programa de Yuca 1973. Cali, Colombia. 287 p.

CIAT. 1976. Sistema de producción de yuca. In: Informe anual 1975. Cali, Colombia. p B1–B59.

CIAT. 1978. Sistema de producción de yuca. In: Informe anual 1977. Cali, Colombia. p C03–C29.

CIAT. 1983a. Almacenamiento de raíces frescas de yuca: Guía de estudio para ser usada como complemento de la unidad audiotutorial sobre el mismo. Cali, Colombia. 35 p.

CIAT. 1983b. Yuca: Bol Info (Cali, Colombia) 1:1–7.

CIAT. 1989. Manejo integrado de *Erinnyis ello* (L.) gusano cachón de la yuca: Guía de estudio, 3a. ed. Cali, Colombia. 62 p.

CIAT. 1990. Annual report [of the] Cassava Program, 1989. Cali, Colombia. 385 p.

CIAT. 1992. Annual report [of the] Cassava Program, 1987–1991. Cali, Colombia. 475 p.

CIAT. 1994. Annual report [of the] Cassava Program, 1993. Cali, Colombia. 325 p.

CIAT. 1995. Annual report [of the] Cassava Program, 1994. Cali, Colombia. p 144–163.

CIAT. 1999. Annual report: integrated pest and disease management in major agroecosystems. Cali, Colombia. 136 p.

D'Almeida YA; Lys JA; Neuenschwander P; Ajuonu O. 1998. Impact of two accidently introduced *Encarsia* species (Hymenoptera: Aphelinidae) and other biotic and abiotic factors on the whitefly *Aleurodicus dispersus* (Russell) (Homoptera: Aleyrodidae) in Benin. Biocontrol Sci Technol 8(1):163–173.

De Morales GJ; de Alencar JA; Wenzel-Neto F; Mergulhão SMR. 1990. Explorations for natural enemies of the cassava green mite en Brazil. In: Proc 8th Symposium International Society of Tropical Root Crops, Bangkok, October 1988. Thai Department of Agriculture; CIAT; Centro Internacional de la Papa (CIP), Bangkok, Thailand. p 351–353.

Delalibera Jr, I; Sosa-Gómez DR; de Morães GJ; Alencar JA; Farias-Araujo W. 1992. Infection of the spider mite *Mononychellus tanajoa* (Acari: Tetranychidae) by the fungus *Neozygites* sp. (Entomophthorales) in Northeast Brazil. Fla Entomol 75(1):145–147.

Dulong R. 1971. Le manioc á Madagascar. Agron Trop 26(8):791–829.

Evans GA; Castillo JA. 1998. Parasites of *Aleurotrachelus socialis* (Homoptera: Aleyrodidae) from Colombia, including descriptions of two new species (Hymenoptera: Aphelinidae: Platygasteridae). Fla Entomol 81(2):171–178.

Farias ARN. 1990. Especies de "mosca blanca": Situação atual e perspective de controle. Centro Nacional de Pesquisa em Mandioca e Fruticultura (CNPMF) of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Cruz das Almas, BA, Brazil. 9 p.

Farias ARN. 1994. Flutuação poblacional de *Aleurothrixus aepim* em mandioca, em São Miguel das Matas, Bahia. Rev Bras Mandioca 13:119–122.

Farias ARN; Sousa JDS; Siweira JRS. 1991. Flutuação populacional de *Bemisia tuberculata* em mora, Gogipe, Bahia. Rev Bras Mandioca 10(1–2):103–107.

Ferreira CF; Alves E; Pestana KN; Junghans DT; Kobayashi AK; Santos VD; Silva RP; Silva PH; Soares E; Fukuda W. 2008. Molecular characterization of cassava with yellow-orange roots for beta-carotene improvement. Crop Breed Appl Biotechnol 8:23–29.

FIDAR (Fundación para la Investigación y el Desarrollo Agrícola). 1998. Reconocimiento e identificación de chisas rizófagas del cultivo de yuca en la zona de ladera del norte del Departamento del Cauca. Folleto divulgativo. FIDAR–PRONATA, Cali, Colombia. 12 p.

França FH; Villas-Boos GL; Branco MC. 1996. Occurrence of *Bemisia argentifolli* Bellow & Perring (Homoptera: Aleyrodidae) in the Federal District. An Soc Entomol Bras 25(2):369–372.

Fregene M; Angel F; Gómez R; Rodríguez F; Chavarriaga P; Roca W; Tohme J; Bonierbale M. 1997. A molecular genetic map of cassava (Manihot esculenta Crantz). Theor Appl Genet 95:431–441.

Frison EA; Feliu E, eds. 1991. Technical guidelines for the safe movement of cassava germplasm. Food and Agriculture Organization of the United Nations (FAO); International Board of Plant Genetic Resources (IBPGR), Rome. 48 p.

Froeschner RC. 1993. The Neotropical lace bugs of the genus *Vatiga* (Heteroptera: Tingidae), pests of cassava: new synonymies and key to species. In: Proc Entomol Soc Wash 95(3):457–462.

García CA; Bellotti AC. 1980. Estudio preliminar de la biología y morfología de *Cyrtomenus bergi* Froeschner: Nueva plaga de la yuca. Rev Colomb Entomol 6(3–4):55–61.

Gold CS. 1993. Effects of cassava intercropping and varietal mixtures on herbivore load, plant growth, and yield: applications for small farmers in Latin America. In: Altieri MA, ed. Crop protection strategies for subsistence farmers. Westview, Boulder, CO, USA. p 117–142.

Gold CS; Altieri MA; Bellotti AC. 1989. Cassava intercropping and pest management: a review illustrated with a case study from Colombia. Trop Pest Manage 35(4):339–344.

Gold CS; Altieri MA; Bellotti AC. 1990. Effects of intercropping and varietal mixtures on the cassava hornworm, *Erinnyis ello* L. (Lepidoptera: Sphingidae), and the stemborer, *Chilomima clarkei* (Amsel) (Lepidoptera: Pyralidae), in Colombia. Trop Pest Manage 36(4):362–367.

Gold CS; Altieri MA; Bellotti AC. 1991. Survivorship of the cassava whiteflies, *Aleurotrachelus socialis* and *Trialeurodes variabilis* (Homoptera: Aleyrodidae) under different cropping systems in Colombia. Crop Prot 10:305–309.

Herren HR; Neuenschwander P. 1991. Biological control of cassava pests in Africa. Annu Rev Entomol 36:257–283.

Herrera CJ. 1999. Manejo integrado de plagas en el cultivo de la yuca. Paper presented at the seminar-workshop "Hacia una producción bioracional de la yuca", held by PMD, IICA, and BIOCARIBE S.A. at Pivijay, Carmen de Bolívar, February 1999. 45 p.

Herrera CJ; Van Driesche RG; Bellotti AC. 1989. Temperature dependent growth rates for the cassava mealybug, *Phenacoccus herreni*, and two of its encyrtid parasitoids, *Epidinocarsis diversicornis* and *Acerophagus coccois* in Colombia. Entomol Exp Appl 50:21–27.

Hershey CH. 1987. Cassava germplasm resources. In: Proc Cassava breeding: a multidisciplinary review, held at Manila, the Philippines, March 1985. CIAT, Cali, Colombia. p 1–24.

Janzen DH. 1986. Biogeography of an exceptional place: what determines the saturniid and sphingiid moth fauna of Santa Rosa National Park, Costa Rica, and what does it mean to conservation biology? Brenesia 25/26:51–87.

Janzen DH. 1987. When and when not to leave. Oikos 49:241–243.

Laberry R. 1997. La aplicación de un programa MIP en producción industrial de yuca. In: Proc Congreso Biodiversidad y Micorrizas. CIAT; Asociación Colombiana de Fitopatología y Ciencias Afines, Cali, Colombia. p 136–137.

Lal SS; Pillai KS. 1981. Cassava pests and their control in southern India. Trop Pest Manage 27(4):480–491.

Le Ru B; Calatayud PA. 1994. Interactions between cassava and arthropod pests. Afr Crop Sci J 2(4):419–421.

Leefmans S. 1915. De cassave-Oerets, vol 13. Mededeelingen van het Laboratorium voor Plantenziekten, Java departement van landbow, Bogor, Indonesia. 120 p.

Leihner DE. 1983. Management and evaluation of intercropping systems with cassava. CIAT, Cali, Colombia. 700 p.

Lohr B. 1983. Biología, ecología, daño económico y control de *Chilomima clarkei* barrenador de la yuca. In: Reyes JA, ed. Yuca: Control integrado de plagas. CIAT, Cali, Colombia. p 159–161.

Lohr B; Varela AM. 1990. Exploration for natural enemies of the cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae), in South America for the biological control of this introduced pest in Africa. Bull Entomol Res 80:417–425.

Londoño M. 1999. Complejo de chisas en Colombia y perspectivas para su manejo. In: Proc XXVI Congress of SOCOLEN, Bogotá, July 1999. SOCOLEN, Bogotá, DC, Colombia.

Londoño M; De los Ríos ML. 1997. Efectos de diferentes agentes de control biológico sobre *Phylophoga obsoleta* y *Anomatha undulata* (Coleoptera: Melolonthidae). In: Antecedentes entomológicos para comprender los insectos: Estudiarlos, GEUN, SOCOLEN, Universidad Nacional–Medellín. Sociedad Colombiana de Entomología, Bogotá, DC, Colombia. p 35–42.

López V, OA; Díaz S, OE; Suárez G, HD; Tolosa P, A. 1996. El barrenador del tallo de la yuca *Chilomima clarkei* (Lepidoptera: Pyralidae) en el CRECED Provincia del Río. Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Bogotá, Colombia 12 p.

Maddison P. 1979. Pests associated with cassava in the Pacific regions: Auckland Pacific Islands pest survey. Entomology Division, Department of Scientific & Industrial Research, Auckland, New Zealand. 16 p.

Magoon ML; Krishnan R; Bai KV. 1969. Morphology of the pachytene chromosomes and meiosis in Manihot esculenta Crantz. Cytologia 34:612–626.

Marín Colorado JA; Ramírez H; Fregene M. 2009. Mapeo genético y análisis de QTL para carotenos en una población S1 de yuca = Genetic mapping and QTL analysis for carotenes in a S1 population of cassava. Acta Agron (Palmira) 58(1):15–21.

Mattos L. 1977. Bacteriosis del tallo de la yuca. MSc thesis. Faculty of Agricultural Sciences, Universidad Nacional Agraria La Molina, Lima, Peru. 83 p.

Morgante M; Salamini F. 2003. From plant genomics to breeding practice. Curr Opin Biotechnol 14:214–219.

Motta E, JC. 1994. Biología y comportamiento alimenticio del gorgojo rojo de la harina *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae), en yuca seca almacenada. Thesis. Universidad Nacional–Palmira, Colombia.

Múnera S, DF; De los Ríos TJ. 1999. Patogenicidad sobre *Erinnyis ello* (L) en condiciones de laboratorio de hongos entomopatógenos recolectados en cultivos comerciales de yuca *Manihot esculenta* Crantz. Rev Colomb Entomol 25(3/4):161–167.

Munthali DC. 1992. Effect of cassava variety on the biology of *Bemisia afer* (Priesner & Hosny) (Hemiptera: Aleyrodidae). Insect Sci Appl 13(3):459–465.

Neuenschwander P. 1994a. Control of cassava mealybug in Africa: lessons from a biological control project. Afr Crop Sci J 2:369–383.

Neuenschwander P. 1994b. Spiralling whitefly *Aleurodicus dispersus*, a recent invader and new cassava pest. Afr Crop Sci J 2(4):419–421.

Nyiira ZM. 1972. Report of investigation of cassava mite, *Mononychellus tanajoa* Bondar. Kawanda Research Station, Kampala, Uganda. 14 p. (Typescript.)

Ogunjobi AA; Fagade OE; Dixon AGO. 2006. Molecular variation in population structure of Xanthomonas axonopodis pv manihotis in the south eastern Nigeria. Afr J Biotechnol 5:1868–1872.

Ortega GA. 2000. Determinación de la efectividad de *Encarsia hispida* De Santis (Hymenoptera: Aphelinidae) como parasitoide de “mosca blanca” de la yuca, *Aleurotrachelus sociali*s Bondar (Homoptera: Aleurodidae), bajo condiciones de invernadero. Thesis. Universidad Nacional–Palmira, Colombia. 89 p.

Parker BL; Booth RH. 1979. Storage of cassava chips (*Manihot esculenta*): insect infestation and damage. Exp Agric 15(2):145–153.

Piedrahíta C. 1986. Empaque y almacenamiento de harina de yuca. Progress report. Proyecto U.V. IIT-CIID.

Polanía MA; Calatayud PA; Bellotti AC. 1999. Comportamiento alimenticio del piojo harinoso *Phenacoccus herreni* (Sternorhyncha: Pseudicoccidae) e influencia del déficit hídrico en plantas de yuca sobre su desarrollo. Rev Colomb Entomol 26(1/2):1–9.

Porter RI. 1988. Evaluation of germplasm (*Manihot esculenta* Crantz) for resistance to the mealybug (*Phenacoccus herreni* Cox and Williams). Dissertation. Cornell University, Ithaca, NY, USA. 117 p.

Renvoize BS. 1973. The area of origin of *Manihot esculen*ta, as a crop plant: a review of the evidence. Econ Bot 26:352–360.

Riis L. 1990. The subterranean burrowing bug *Cyrtomenus bergi* Froeschner, an increasing pest in tropical Latin America: behavioral studies, population fluctuations, botanical control, with special reference to cassava. MSc thesis. Zoology Section of the Institute of Ecological and Molecular Biology, Royal Veterinary and Agricultural University, Copenhagen, Denmark. 167 p.

Riis L. 1997. Behaviour and population growth of the burrower bug, *Cyrtomenus bergi* Froeschner: effects of host plants and abiotic factors. Dissertation. Royal Veterinary and Agricultural University, Copenhagen, Denmark. 167 p.

Riis L; Bellotti AC; Vargas O. 1995. The response of a polyphagous pest (*Cyrtomenus bergi* Froeschner) to cassava cultivars with variable HCN content in root parenchyma and peel. In: Proc Second International Scientific Meeting of the Cassava Biotechnology Network, Bogor, Indonesia, Aug 1994. CIAT, Cali, Colombia. p 501–509.

Román A. 1983. Secado natural, una solución al mercadeo de la yuca. Yuca Bol Inf 7(1):57–88.

Sánchez D; Bellotti AC. 1997a. Evaluación de la patogenicidad de hongos *Hyphomycetes* sobre mosca blanca de la yuca *A. socialis.* Report of the Convenio Cooperativo CIAT-COLCIENCIAS, Programa COLCIENCIAS-BID para jóvenes investigadores. 20 p.

Schoonhoven A van. 1974. Resistant to thrips damage in cassava. J Econ Entomol 67(6):728–730.

Skovgard H; Tomkiewicz J; Nachman G; Münster-Swendsen M. 1993. The effect of the cassava green mite *Mononychellus tanajoa* on the growth and yield of cassava *Manihot esculenta* in a seasonally dry area in Kenya. Exp Appl Acarol 17(1/2):41–58.

Smith L; Bellotti AC. 1996. Successful biocontrol projects with emphasis on the Neotropics. In: Proc Cornell Communications Conference on Biological Control, held at Cornell University, April 1996. Cornell University Press, Ithaca, NY, USA. 12 p.

Swaine G. 1950. The biology and control of the cassava scale. East Afr Agric J 16:90–93.

Tejada GAP. 1975. Identificación morfológica y algunos aspectos ecológicos de tres especies de trips, en variedades resistentes y susceptibles de yuca (*Manihot esculenta* Crantz). Thesis. Faculty of Agricultural Sciences, Universidad Nacional–Palmira, Colombia. 83 p.

Thresh JM; Fargette D; Otim-Nape GW. 1994. Effects of African cassava mosaic geminivirus on the yields of cassava. Trop Sci 34:26–42.

Urías-López, MA; Bellotti AC; Bravo M, H; Carrillo S, JL. 1987. Impacto de insecticidas sobre tres parasitoides de *Erinnyis ello* (L.), gusano de cuerno de la yuca. Agrociencia 67:137–146.

Van Driesche RG; Castillo JA; Bellotti AC. 1988. Field placement of mealybug-infested potted cassava plants for the study of parasitism of *Phenacoccus herreni*. Entomol Exp Appl 46:117–123.

Van Driesche RG; Bellotti AC; Castillo JA; Herrera CJ. 1990. Estimating total losses from parasitoids for a field population of a continuously breeding insect, cassava mealybug, *Phenacoccus herreni* (Homoptera: Pseudococcidae) in Colombia, SA. Fla Entomol 73(1):133–143.

Vargas O; Bellotti AC. 1981. Pérdidas en rendimiento causadas por moscas blancas en el cultivo de la yuca. Rev Colomb Entomol 7(1/2):13–20.

Victoria JAT; Pardo LC. 1999. Avances en el estudio de las chisas (Coleoptera: Melolonthidae) observadas en la rizosfera de yuca y otros cultivos en tres municipios del Cauca, Colombia.

Vidal JG; Marín H. 1974. Identificación y ciclo biológico de un díptero barrenador de la yuca (*Manihot esculenta* Crantz). Thesis. Faculty of Agricultural Sciences, Universidad Nacional–Palmira, Colombia. 45 p.

Villegas AG. 1984. Biología, morfología, y hábitos de *Lagocheirus araneiformis* Linné (Coleoptera: Cerambycidae) barrenador de la yuca en Palmira, Valle del Cauca. Thesis. Universidad Nacional–Palmira, Colombia. 68 p.

Williams DJ; Granara de Willink MC. 1992. Mealybugs of Central and South America. CAB International, Wallingford, UK. 635 p.

Yaninek JS. 1988. Continental dispersal of the cassava green mite, an exotic pest in Africa, and implications for biological control. Exp Appl Acarol 4:211–224.

Yaninek JS; Animashaun A. 1987. Why cassava green mites are dry season pests. Proc seminar on Agrometeorology crop protection in lowland humid and sub-humid tropics, held by the World Meteorological Organization (WMO) and International Institute of Tropical Agriculture (IITA), Contonou, Benin, July 1986. International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. p 59–66.

Yaninek JS; Herren HR. 1988. Introduction and spread of the cassava greenmite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae), an exotic pest in Africa, and the search for appropriate control methods: a review. Bull Entomol Res 78(1):1–13.

Yaninek JS; Mégev B; de Morães GJ; Bakker F; Braun A. 1991. Establishment of the Neotropical predator *Amblyseius idaeus* (Acari: Phytoseiidae) in Benin, West Africa. Biocontrol Sci Technol 1(4):323–330.

Yaninek JS; Onzo A; Ojo JB. 1993. Continent-wide releases of Neotropical phytoseiids against the exotic cassava green mite in Africa. Exp Appl Acarol 17(1/2):145–160.

Yaninek JS; Saizonou S; Onzo A; Zannou I; Gnanvossou D. 1996. Seasonal and habitat variability in the fungal pathogens, *Neozygites* cf. *floridana* and *Hirsutella thompsonii*, associated with cassava mites in Benin, West Africa. Biocontrol Sci Technol 6(1):23–33.