BIOLOGICAL CONTROL OF THE CASSAVA HORNWORM *ERINNYIS ELLO* (LEPIDOPTERA: SPHINGIDAE)

A. C. BELLOTTI, B. ARIAS V., AND O. L. GUZMAN
Centro Internacional de Agricultura Tropical (CIAT)
Apartado Aéreo 6713 Cali, Colombia

ABSTRACT

Several Lepidoptera attack cassava; of these the cassava hornworm, *Erinnyis ello* (L) (Sphingidae), is the only serious lepidopteran pest throughout the cassava-growing regions of the Neotropics. Severe attacks cause complete plant defoliation, losses in bulk root production, and lower root quality. Hornworm attacks may be sporadic, are often cyclic and usually unpredictable. Farmers often react to severe attacks by excessive, ill-timed applications of pesticides that may result in resurgence of this pest. Biological control offers an economically feasible and environmentally sound alternative. Approximately 40 natural enemies have been identified including egg and larval parasites, egg, larval, and pupal predators, fungi, bacteria and a virus. Because of the migratory behavior of hornworm adults, this abundance of natural enemies does not prevent periodic hornworm outbreaks. A hornworm baculovirus is highly effective in control of *E. ello*, and is being utilized by cassava farmers in southern Brazil.

RESUMEN

Varios lepidopteros atacan la yuca, uno de estos es el gusano cachon *Ernnyis ello* (L) (Sphingidae) el cual es la unica plaga lepidoptera importante en todas las regiones yuqueras del neotropico. Ataques severos causan defoliacion completa de la planta, disminucion en tamano de raices y baja calidad de las mismas. Los ataques de gusano cachon pueden ser esporadicos, a menudo son ciclicos y generalmente impredecibles. Los agricultores reaccionan frequentemente a los ataques de cachon mediante aplicaciones excesivas de pesticidas, lo cual puede originar ataques mas frequentes. El control biologico ofrece una buena y factible alternativa que favorece ademas el medio ambiente. Aproximadamente 40 enemigos naturales han sido identificados incluyendo parasitos de huevos y larvas, predadores en huevos, larvas y pupas, ademas de hongos, bacterias y virus. Debido a el comportamiento migratorio de los adultos de gusano cachon, dicha abundancia de enemigos naturales no previene las explosiones periodicas del mencionado insecto. El Baculovirus es altamente efectivo en el control de *E. ello*, y actualmente viene siendo utilizado por los agricultores productores de yuca.

Cassava (*Manihot esculenta* Crantz) is a perennial euphorbiaceus shrub grown commercially as an annual or biennial. Its long vegetative cycle makes it particularly vulnerable to attack by a wide range of arthropod pests (Bellotti & Schoonhoven 1978). Several species of Lepidoptera feed on cassava, including *Erinnyis ello* (L), *Chilomina clarkei* (Amsel), *Chilozela bifilalis* (Hampson), *Phyctaenodes fibilialis*, *Agrotis ipsilon*, *Prodenia eridania* and *Phoenicoprocta sanguinea*.

The stemborer, *C. clarkei*, causes breakage of cassava stems. Infestations which result in more than 35% stem breakage can cause root yield reductions (CIAT 1981). *A. ipsilon* and *P. eridania* can attack recently planted stem cuttings of this vegetatively propagated by crop, resulting in poor germination. *P. sanguinea* is a leaf feeder, however, yield reduction attributable to this species has not been documented (CIAT 1982).

The cassava hornworm, *E. ello* (Sphingidae), is one of the most serious pests of cassava in the Neotropics. *E. ello* has a broad geographical range, extending from

southern Brazil, Argentina and Paraguay to the Caribbean basin and the southern United States (Winder 1976). Although several species of *Erinnyis* feed on cassava, *E. ello* is the most commonly reported species. The sub-species *E. ello ello* is reported from the Neotropics and Neoartic, and *E. ello encantado* is reported from the Galapagos Islands (Carvalho 1980).

Farmers often react to attacks by excessive, ill-timed applications of pesticides, which can lead to repeated and more severe attacks (Bellotti & Schoonhoven 1978). Adequate host plant resistance to *E. ello* is not available, although ovipositional non-preference has been detected (Bellotti & Arias 1988). An extensive complex of natural enemies is associated with *E. ello*, nevertheless, sporadic and unpredictable attacks often occur when natural enemy population levels are low and thus unable to prevent severe outbreaks. Careful monitoring of hornworm populations together with manipulation and management of natural enemies is the key for successful control of *E. ello*.

Hornworm larvae feed on cassava leaves of all ages, and on the young tender growing stem and leaf buds. Severe attacks cause complete plant defoliation, bulk root loss and poor root quality. Losses in root production are influenced by plant age, soil fertility, environmental factors (especially rainfall) and frequency of attacks. In simulated damage studies, yield losses in fertile soils ranged from 0 to 25% for one attack, and up to 47% after two consecutive attacks. On less fertile soils, losses between 15 and 45% for one attack and up to 64% after two attacks have been reported (Arias & Bellotti 1984). These data indicate that although yield losses may be severe, complete defoliation due to hornworm attack or even repeated attacks, does not kill cassava. The carbohydrates stored in the roots enable the plant to recover, especially during the more favorable conditions of the tropical rainy season. Repeated attacks are most common when ill-timed pesticide applications do not destroy fifth instar larvae or prepupae, but destroy the natural enemies that are present during its initial hornworm outbreak (Bellotti, pers. obs.). During its larval period, each hornworm consumes approximately 1100 cm^2 of leaf foliage; about 75% of this is ingested during the fifth instar stage.

Hornworm Biology, Ecology and Behavior

Hornworm adults are grey nocturnal moths that oviposit small round, light green to yellow eggs individually on the upper surface of cassava leaves (Gold et al. 1989). Eggs hatch in 3 to 5 days. In field cage studies females oviposited an average of 450 eggs, although as many as 1850 eggs per female were observed. This partially explains the rapid build-up of hornworm populations. At 15, 20, 25 and 30°C the mean length of the larval stage is 105, 52, 29 and 23 days respectively, suggesting that peak hornworm activity should occur in lowland to middle (800 to 1200 masl) altitudes in the tropics and in the subtropics during the summer periods (Bellotti & Arias 1988).

Observations on the seasonal abundance of *E. ello* in cassava indicate that outbreaks may occur sporadically, but usually coincide with the rainy season when young foliage is present (Fig. 1). Janzen (1987) has observed that climatic conditions play an important role in hornworm migration and population dynamics. In subtropical zones, *E. ello* is generally absent during the winter and usually reappears during summer (Bellotti per. obs.). When considerable leaf area is present, up to 600 eggs may be found in a single plant, with an average of 150. Larval populations may exceed 100 per plant (Bellotti et al. 1983). The number of larvae needed for complete plant defoliation depends on several factors related to plant growth and soil fertility. On infertile soils, 4.5 fifth instar larvae defoliate a one-month old plant, and 13 larvae a three month old plant in 3 to 4 days. On fertile soils a higher larval density was required for defoliation due to more abundant leaf production (Arias & Bellotti 1984). Since cassava is grown primarily on low fertility soils, hornworm outbreaks must be controlled when populations are in the early larval stages.

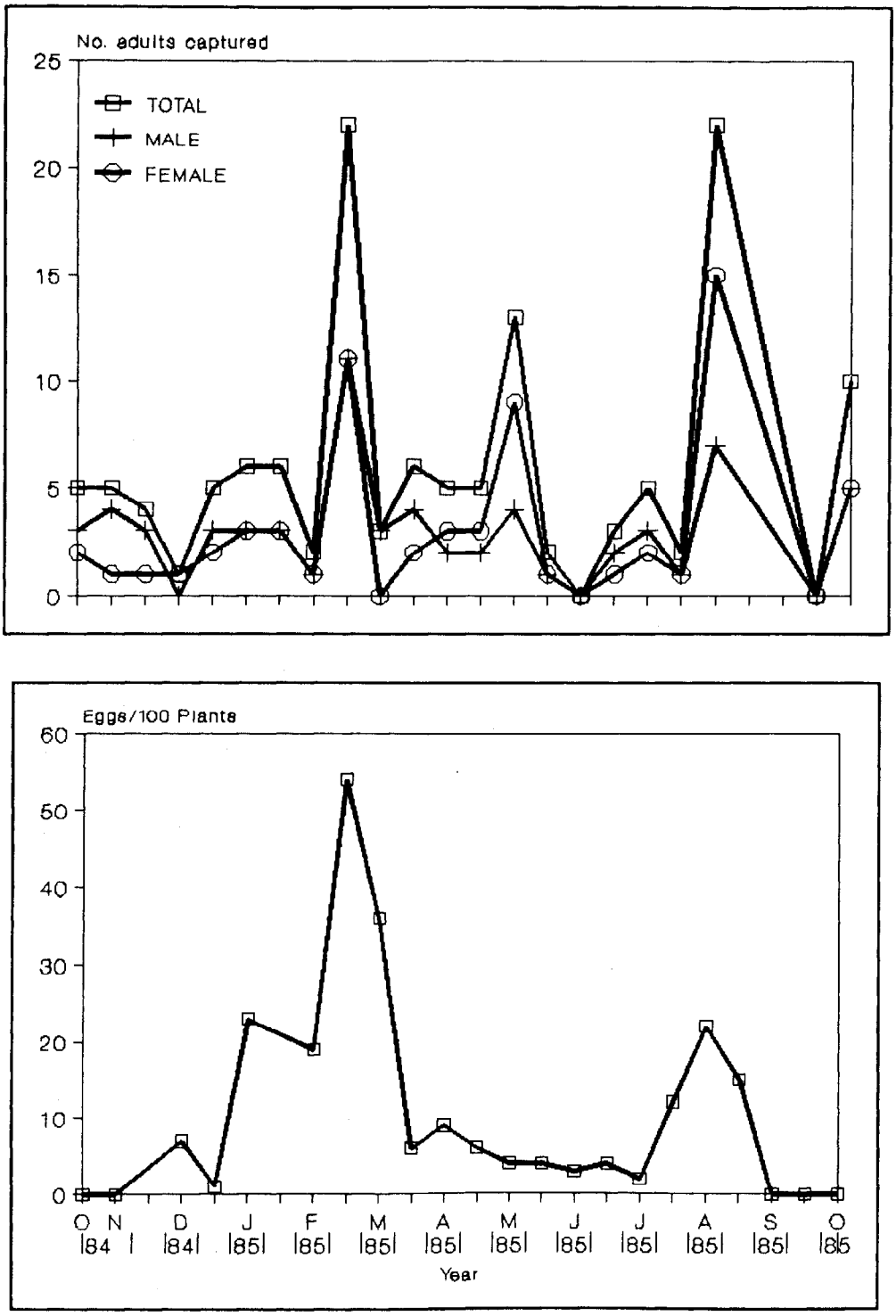

Fig. 1. Light trap capture of *E. ello* adults and corresponding oviposition on cassava plants (CIAT 1984-85).

The migratory flight capacity of *E. ello* is well documented (Winder & Abreu 1976, Janzen 1986, 1987). Its strong flight abilities (Wolda 1979), broad climatic adaptation and wide host range (Janzen 1985) probably account for its distribution throughout the Neotropics. Larvae have been reported feeding on 35 different hosts in 10 families including papaya, tomato, tobacco, and cotton (Winder 1976). Adults migrating *en masse* will oviposit a considerable number of eggs in cassava fields (Bellotti et al. 1983). "Invasions" have been detected in light trap surveys in Colombia, Brazil, Cuba, and Mexico (Bellotti pers. obs.) and result in explosions of hornworm larvae which can cause severe crop defoliation and yield reduction.

Insect migration has been described as an evolved adaptation for survival and reproduction (Johnson 1960) and attributed to stimuli such as low food availability, high hornworm density, unfavorable environmental conditions and the presence of natural enemies (Wallner 1987, Andrewartha & Birch 1982). We speculate that effectiveness of natural enemies is greatly reduced due to the migratory behavior of hornworm adults. Because their rate of reproduction is limited, predators and parasites usually cannot compensate quickly enough to suppress dramatic pest irruptions of certain migratory Lepidoptera (Wallner 1987). A combination of these factors undoubtedly plays a role in hornworm outbreaks and hinders effective *E. ello* control.

Biological Control of *E. ello*

More than 30 species of parasites, predators and pathogens of the egg, larval, and pupal stages have been identified (Table 1). *Trichogramma* spp. and *Telenomus* spp. are the most important egg parasites (Winder 1976, Bellotti & Arias 1988). A three year study in the Cauca Valley of Colombia estimated egg parasitism at between 53 and 57%. With high hornworm populations this is not sufficient to reduce larval numbers below economic injury levels (Bellotti et al. 1983, Bellotti & Arias 1988). Releases of *Trichogramma* spp. to augment natural parasitism will significantly increase levels of egg parasitism. However, *Trichogramma* prefers to parasitize recently oviposited *E. ello* eggs. Hence, the availability of sufficient *Trichogramma* and the difficulty of synchronizing release to coincide with *E. ello* oviposition limits their use, especially for resource-limited cassava farmers.

Telenomus egg parasites are larger than *Trichogramma* spp. and possess greater searching capacity (Gold et al. 1989). Each *Telenomus* parasitizes an average of 32 hornworm eggs. *Telenomus* spp., however, are more difficult to rear on a large scale, compared to *Trichogramma*, and therefore the latter is preferred (Bellotti et al. 1983).

Tachinid flies are the most important dipteran parasites (Winder 1976), and the Braconidae, particularly *Apanteles* spp. are the most important hymenopteran, larval parasites of the hornworm. Field studies (CIAT 1978) showed that *Apanteles* spp. releases increased larval parasitism to 27%; however, high levels of hyperparasitism associated with *Apanteles* spp. reduce their effectiveness in the field.

Although several predator species feed on hornworm eggs, larvae, and pupae, few have been studied in detail. The most common egg predators are *Chrysopa* spp. One larva can consume 17 hornworm eggs per day.

The most important larval predators are *Polistes* spp. (Hymenoptera: Vespidae), *Podisus* spp. (Hemiptera: Pentatomidae) and a number of spider species. *Polistes erythrocephalus* generally live in small colonies in or around cassava fields. Their sting paralyses hornworm larvae. Larvae too large to transport are sectioned into strips, rolled up, and carried to the nest. *Polistes* predation levels are primarily determined by the number of wasp larvae contained in the nest and not necessarily by the availability of other prey species. Each *Polistes* larva consumes ca. 0.5 hornworm larvae daily (Bellotti & Arias 1988). *Polistes* can be maintained in cassava fields by constructing roofed, open-sided huts to encourage and protect wasp colonies.

TABLE 1. PARASITES, PREDATORS AND PATHOGENS OF *ERINNYIS ELLO* (L).

Natural Enemy Stage Attacked	Behavior	Order	Family
Egg			
Trichogramma minutum	Parasitoid	Hymenoptera	Trichogrammatidae
T. fasciatum	Parasitoid	Hymenoptera	Trichogrammatidae
T. exiguum	Parasitoid	Hymenoptera	Trichogrammatidae
T. semifumatum	Parasitoid	Hymenoptera	Trichogrammatidae
Telenomus dilophonatae	Parasitoid	Hymenoptera	Scelionidae
T. sphingis	Parasitoid	Hymenoptera	Scelionidae
Ooencyrtus submetalicus	Parasitoid	Hymenoptera	Encyrtidae
Ooencyrtus sp.	Parasitoid	Hymenoptera	Encyrtidae
Chrysopa sp.	Predator	Neuroptera	Crysopidae
Dolichoderus sp.	Predator	Hymenoptera	Formicidae
Larvae			
Apanteles congregatus	Parasitoid	Hymenoptera	Braconidae
A. americanus	Parasitoid	Hymenoptera	Braconidae
Euplectrus sp.	Parasitoid	Hymenoptera	Eulophidae
Cryptophion sp.	Parasitoid	Hymenoptera	Ichneumonidae
Microgaster flaviventris	Parasitoid	Hymenoptera	Ichneumonidae
Sarcodexia innota	Parasitoid	Diptera	Sarcophagidae
Chatogena (Euphorocera) *scutelaris*	Parasitoid	Diptera	Tachinidae
Thysanomyia sp. *Belvosia* sp.	Parasitoid	Diptera	Tachinidae
Drino macarensis	Parasitoid	Diptera	Tachinidae
Polistes erythrocephalus	Predator	Hymenoptera	Vespidae
P. versicolor	Predator	Hymenoptera	Vespidae
P. carnifex	Predator	Hymenoptera	Vespidae
P. canadensis	Predator	Hymenoptera	Vespidae
Polybia sericea	Predator	Hymenoptera	Vespidae
Podisus nigrispinus	Predator	Hemiptera	Pentatomidae
Podisus sp.	Predator	Hemiptera	Pentatomidae
Zellus sp.	Predator	Hemiptera	Reduviidae
Alcaeorrhynchus grandis	Predator	Hemiptera	Pentatomidae
Bacillus thuringiensis	Pathogen	Eubacteriales	Bacillaceae
Baculovirus	Pathogen	Nuclear Granuloses	
Prepupae Pupae			
Calosoma sp.	Predator	Coleoptera	Carabidae
Pupae			
Cordyceps	Pathogen	Schaeriales	Hypocreaceae
	Predators	Arachnida	Tomicidae
Others			Salticidae

Predator effectiveness in hornworm control is limited by poor functional response during hornworm outbreaks, which are of short duration (about 15 days). The release of predators to augment field populations is not economically feasible. Natural field populations of predators are seldom sufficient to control hornworm outbreaks effectively.

Cordyceps sp. (Ascomycetes: Clavicipitaceae) a soil-borne fungus, invades hornworm pupae causing mortality. The fungus can be cultured in the laboratory on oat-agar media. In controlled experiments in Colombian cassava fields, inoculation of soil with the fungus resulted in 80% mortality of hornworm pupae (Bellotti & Arias 1988). Since a generation of larvae has already caused plant defoliation by the time they enter susceptible pupal stage, the potential of *Cordyceps* as a biological control agent is limited.

The bacterial pesticide, *Bacillus thuringiensis* is effective in controlling hornworm larvae (Bellotti & Arias 1988). Larval mortality reached 68% in field studies 3 days after application. The bacterium is most effective against the first three larval instars.

A granulosis virus of the family Baculoviridae was found attacking *E. ello* larvae in CIAT cassava fields in the early 1970's. Identification of the virus was done at Boyce Thompson Institute (Cornell University, Ithaca, N.Y.) (Granados, pers. comm.) Subsequent studies have determined the value and potential of this virus for *E. ello* control (Arias & Bellotti 1987, Bellotti & Arias 1988, Bellotti et al. 1990, Schmidt 1988).

Early pathogenicity studies involved collecting infected larvae from the field, liquefying these in a blender and filtering the mixture through cheesecloth. The resulting liquid was diluted with water and applied to cassava plants in the field. First, second and third instar hornworm larvae were released in virus-infected fields. After for 24 hours, they were collected and maintained on clean cassava leaves in the laboratory. After 72 hours larval mortality reached 100% (Bellotti et al. 1990).

In a field trial in El Patia, Colombia, freshly collected virus was prepared at a concentration of 70 grams (prepared as previously described) in 200 l of water and applied to hornworm-infested fields. Hornworm numbers were monitored on 50 plants in treated and non-treated plots before and 48 hours after application. Mortality at 48 hours was 99.8% (Bellotti et al. 1990).

Storage of the virus is feasible. Virus obtained from hornworms frozen for four years resulted in 67% control in field trials. Lyophilized virus stored for two years resulted in only 27% mortality (Bellotti et al. 1990). Virus extracted from recently collected infected hornworms resulted in 100% mortality.

The effect of virus concentration and larval instar on mortality were evaluated after 72, 96, 120 and 144 h. Ninety percent mortality was obtained with the 0.9 ml virus/l water (1.5×10^6 inclusion bodies IB) (Fig. 2). A sigmoidal relationship between concentration and mortality was found for the first, second, and fourth instars in the range of concentrations tested. Most fifth instar larvae reached the prepupal stage. At the lowest concentration (1.85×10^4 IB/l water) 30% mortality occurred and 52.5% mortality was obtained at the highest concentration (4.5×10^6 IB/l water) (Table 2). At the lowest concentration 60% of the prepupa reached the pupal stage while only 27.5% pupated at the highest concentration. Considerable pupal deformity was observed. Adult emergence from the pupal stage was 45% at the lowest and 15% at the highest concentration (Table 2). Wing deformity was common in adults. Very few female adults emerged and these died without producing progeny. These data indicate that virus applications to fifth instar larvae can effectively reduce subsequent hornworm populations.

The lowest LC_{50} (8.88×10^4 IB/l water) was associated with first instar larvae. LC_{50} increased to 1.71×10^6 IB/l water (Table 3) for fourth instar larvae, indicating that progressively higher concentrations are needed for adequate control of each succeeding hornworm larval instar.

The persistence of the virus was determined after application of a 20% virus solution to cassava fields. At 0, 1, 5, 9, 13 and 19 days after application leaves were removed and placed in petri dishes in the laboratory and fed to first instar larvae. Twenty-four h after application mortality was 96%, declining to 11% after 19 days. At 9.4 days after application, 50% mortality was attained (Fig. 3). There was no significant difference in mortality between virus preparations applied with or without an adjuvant.

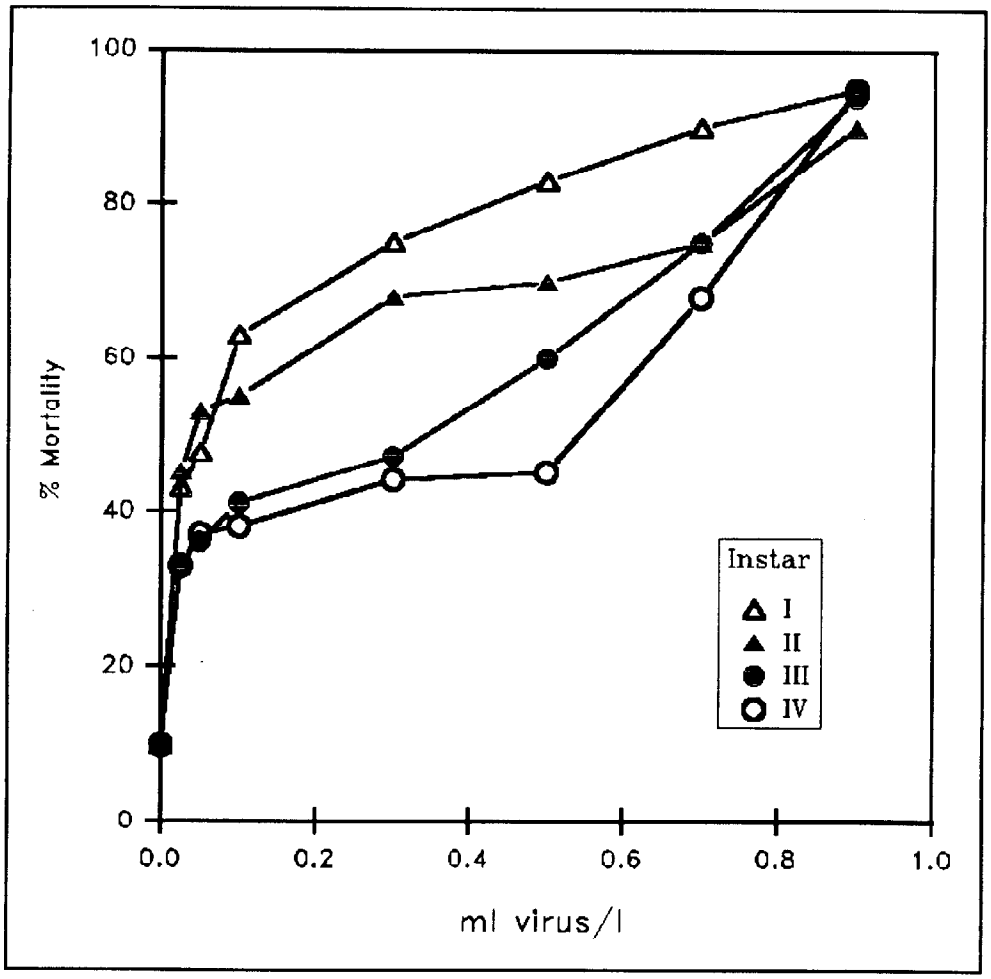

Fig. 2. Effect of virus concentrations on mortality of *E. ello* instars. LC_{50} = .05 ml virus/l for instars III (95% CI: .03 – .07 ml virus/l) and IV (95% CI: .02 – .09 ml virus/l) significant departure from the probit model was observed for instars I and II.

TABLE 2. EFFECT OF CONCENTRATION OF *BACULOVIRUS* ON SURVIVAL OF PUPAL AND ADULT *E. ELLO*.

No. inclusions bodies/L H_2O	% Mortality		
	Prepupa	Pupa	Adult
1.85×10^4	30.0	40.0	55.0
7.4×10^4	40.0	55.0	62.5
2.2×10^5	45.0	60.0	70.0
6.8×10^5	45.0	60.0	70.0
1.9×10^6	47.5	67.5	75.0
3.3×10^6	42.5	72.5	82.5
4.5×10^6	42.5	72.5	85.0
Control	15.0	20.0	42.5

TABLE 3. AVERAGE LETHAL CONCENTRATION (LC_{50}) OF *BACULOVIRUS* FOR 4 LARVAL INSTARS OF *E. ELLO*.

Instar	ML Virus/l H_2O	Inclusion bodies Virus/l H_2O
I	0.06	8.88×10^4
II	0.11	2.42×10^5
III	0.22	4.84×10^5
IV	0.45	1.71×10^6

DISCUSSION

Cassava production, especially in Coastal Ecuador, Colombia and Northeastern Brazil is expanding and intensifying. Historically the intensification of production has been accompanied by increased insecticide use. Pesticide use in cassava is negligible at present, however, increased hornworm attacks could lead to increases in pesticide applications.

Natural biological control is ineffective in preventing outbreaks due to the migratory behavior of adults. During these relatively brief but severe "invasions", native natural enemies, which are in equilibrium with small hornworm populations, do not increase rapidly enough for effective control of hornworm larvae. Although pesticide applications can bring hornworm irruptions under control, they are costly and toxic to natural enemies (Urias et al. 1987).

For biological control to be effective under these conditions, native natural enemy populations must be augmented when adult invasions occur. Two guidelines for this are; 1) hornworm irruptions must be detected at the earliest opportunity, preferably the

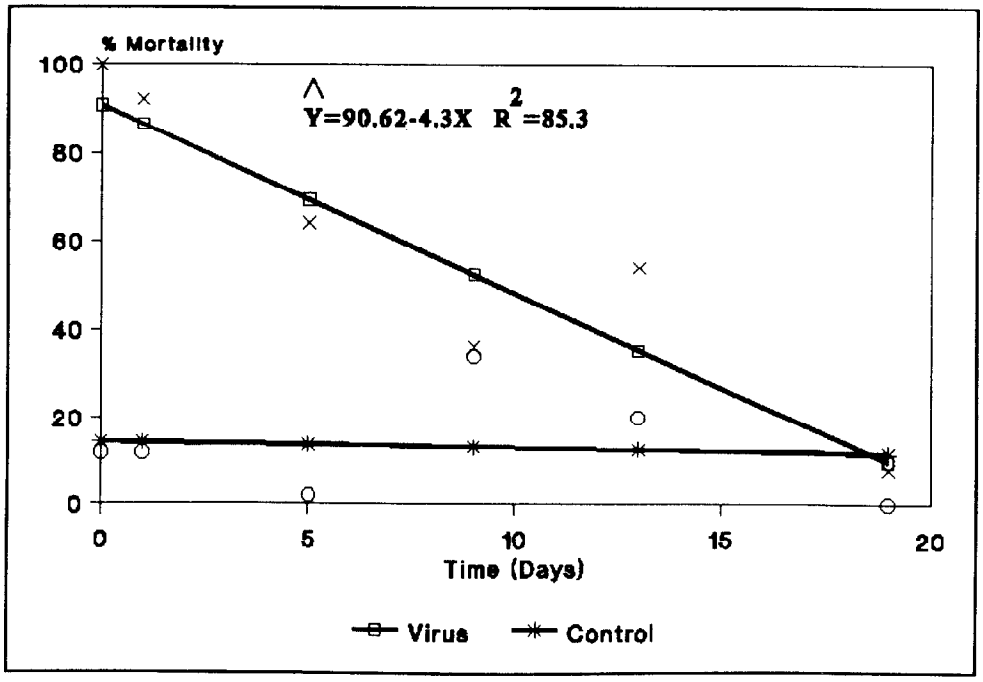

Fig. 3. Persistance of hornworm baculovirus under field conditions.

immigrant adult or egg stage; and 2) an easily manageable natural enemy must be available for introduction during the early stages of larval feeding. Adult invasions can be detected with light traps (Black light, type T20T12BLT) operated between midnight and 2 am, the hours of peak activity for hornworm adults (Bellotti & Arias 1988). Hornworm eggs are easily visible on the upper surface of young cassava leaves. Weekly field inspections during likely periods of hornworm invasion, particularly at the initiation of the rainy season, assist greatly in detecting hornworm outbreaks.

The hornworm virus provides an attractive management option due to its ease of manipulation and storage, and low cost. Whereas populations of parasites or predators would have to be continually maintained in culture under controlled conditions, the virus can be maintained in refrigerated liquid form until required for field application. The need to maintain a perpetual culture of parasites or predators is avoided. The simple application method (back-pack sprayer), and the ease of maintaining a supply of virus by collecting infected larvae from the field for storage are additional advantages. Through early detection of hornworm attacks the virus can be applied while larval populations are in the early instars which are susceptible to low concentrations of the virus.

The implementation of these techniques for the biological control of *E. ello* has been achieved in southern Brazil where frequent hornworm outbreaks cause considerable yield losses. In southern Brazil, the strategy for a successful control program consists of several steps involving the coordination of various entities. Research on the storage and application of the virus was done by EMPASC (Empresa de Pesquisa Agropecuaria de Santa Catarina) (Schmidt 1988) in collaboration with CIAT. Farmers and industry personnel were trained by researchers and extension service specialists in the storage and use of the virus. Light traps were placed in key locations throughout the zone to detect presence and movement of *E. ello* adults. The virus was multiplied and stored by the research and extension service as well as by cassava grower cooperatives and the cassava processing industry. This industry has its own extension personnel and has contracts for cassava production with farmers. Field monitoring and field inspections are encouraged. Virus applications are timed to coincide with the presence of the first three larval instars. Trials in farmers fields in Santa Catarina, Brazil, resulted in 100% hornworm control over a six day period (Schmidt 1988). The *E. ello* virus combined with timely detection of hornworm outbreaks provides an effective and economical control of this pest. In Parana, Brazil pesticide applications for hornworm control were reduced by 60%. The costs of applying pyrethroids was calculated at US$14.00/ha vs US$1.00/ha for the hornworm virus (Torrecillos, pers. com). Similar programs are being developed in the north coast of Colombia and areas of Central America and the Caribbean.

References Cited

ANDREWARTHA, H. G., AND L. C. BIRCH. 1982. Theory of the distribution of abundance of animals, pp. 185-221 *in* The ecological web: More on the distribution and abundance of animals. Chicago Univ. Press.

ARIAS, B., AND A. C. BELLOTTI. 1984. Perdidas en rendimiento (daño simulado) causadas por *Erinnyis ello* (L) y niveles criticos de poblacion en diferentes etapas de desarrollo en tres clones de yuca. Rev. Col. de Entomol. 10(3 & 4) p 28-35.

ARIAS, B., AND A. C. BELLOTTI. 1987. Control de *Erinnyis ello* (L) (Lep: Sphingidae) gusano cachon de la yuca, *Manihot esculenta* (Crantz) con *Baculovirus erinnyis* NGV. Rev. Col. Entomol. 13(2) P. 29-35.

BELLOTTI, A. C. AND A. VAN SCHOONHOVEN. 1978. Mite and insect pests of cassava. Ann. Rev. Entomol. 23: 39-67.

BELLOTTI, A. C., J. A. REYES, B. ARIAS, P. SEGURA, M. A. URIAS, AND A. T. SCHMIDT. 1983. Manejo de una explosion de gusano cachon, *Erinnyis ello* (L) (Lep: Sphingidae), pp. 205-312 *in* J. A. Reyes [ed.], Yuca: Control Integrado de las Plagas. PNUD: CIAT, Cali, Colombia, 362 pp.

BELLOTTI, A. C., AND B. ARIAS, V. 1988. Manejo integrado de *Erinnyis ello* (L). Serie: 04SC-04.01 CIAT, Cali, Colombia.

BELLOTTI, A. C., B. ARIAS, V., AND J. A. REYES. 1990. Biological control of the cassava hornworm, *Erinnyis ello* (Lepidoptera: Sphingidae) with emphasis on the hornworm virus, pp. 354-362 *in* R. H. Howeler [ed.], Pro. 8th. Simp. Int. Soc. Trop. Root. & Tuber Crops. Bangkok, Thailand, 1988.

CARVALHO, C. F. 1980. Aspectos biologicos, tecnicos para obtencao de ovos em condicoes de laboratorio e availacao de danos de *Erinnyis ello* (Linnaeus, 1758) (Lepidoptera-Sphingidae) em mandioca em condicoes de campo. Tese Mag. Sc. Piracicaba. SP, Luis de Queiroz. 87p Port.

CENTRO INTERNACIONAL DE AGRICULTURA TROPICAL (CIAT). 1978. Cassava production systems. Annual Report, 1978. CIAT, Cali, Colombia.

———. 1981. Cassava production systems. Annual Report, 1981. CIAT, Cali, Colombia.

———. 1982. Cassava production systems. Annual Report, 1982. CIAT, Cali, Colombia.

———. 1990. Cassava production systems. Annual Report, 1990. CIAT, Cali, Colombia.

GOLD, C. S., M. A., ALTIERI, AND A. C. BELLOTTI. 1989. Relative oviposition rates of the cassava hornworm, *Erinnyis ello* (Lep.: Sphingidae), and accompanying parasitism by *Telenomus sphingis* (Hym.: Scalinidae), on upper and lower leaf surfaces of Cassava. Entomophaga 34(1): 73-76.

JANZEN, D. H. 1985. A host plant is more than its chemistry. Illinois National History Survey Bull. Vol. 33. Art. 3.

JANZEN, D. H. 1986. Biogeography of an unexceptional place: what determines the saturniid and sphingid moth fauna of Santa Rosa National Park, Costa Rica, and what does it means to conservation biology. Brenesia. 25/26:51/87.

JANZEN, D. H. 1987. When and when not to leave. OIKOS 49: 241-243. Copenhagen.

JOHNSON, C. G. 1960. A basis for a general system of insect migration and dispersal by flight. Nature 186: 348-350.

SCHMIDT, A. T. 1988. Uso de *Baculovirus erinnyis* para el control biologico del gusano cachon de la yuca. Yuca Boletin Informativo. Vol. 12: 1.

URIAS, M. A., A. C. BELLOTTI, H. BRAVO MOJICA, AND J. L. CARRILLO SANCHEZ. 1987. Impacto de insecticidas sobre tres parasitoides de *Erinnyis ello* (L), gusano de cuerno de la yuca. Agrociencia Num. 67: 137-146.

WALLNER, W. E. 1987. Factors affecting insect population dynamics: differences between outbreak and new outbreak species. Ann. Rev. Entomol. 32: 317-340.

WINDER, J. A. 1976. Ecology and control of *Erinnyis ello* and *E. alope* important insect pests in the New World. PANS 2(4): 449-466.

WINDER, J. A., AND J. M. DE ABREU. 1976. Preliminary observations on the flight behavior of the Sphingid moths *Erinnyis ello* L. and *E. alope* Drury (Lepidoptera), based on light trapping. Ciencia e cultura 28: 444-448.

WOLDA, H. 1979. Fluctuaciones estacionales de insectos en el tropico: Sphingidae, Memorias del Congreso de la Sociedad Colombiana de Entomologia. Julio 25-27, 1979. Cali, Colombia.