Life History and Ecology of the Moth *Sameodes albiguttalis*,[1] a Candidate for Biological Control of Waterhyacinth[2]

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ABSTRACT

Larvae of the pyralid moth, *Sameodes albiguttalis* (Warren), caused heavy but sporadic damage to waterhyacinth, *Eichhornia crassipes* (Mart.) Solms in Argentina. Females laid an avg of 300 eggs each, usually in injuries, on the plant leaves. The larvae fed inside the petioles and bud of the plant and pupated in white cocoons in the bulbous-type petioles. Eggs required 4 days to hatch, the 5 larval instars took a total of 21 days to pupate, and pupae took 7 days to emerge. In the laboratory, 95.6% of the eggs survived, 54.3% of the larvae, and 96% of the pupae. With optimum conditions in the laboratory, the population was calculated to increase 1.16 times/day, or 150 times/generation of 34 days, and to double each 4.7 days. Five generations/year occurred in the field, and maximum populations measured were 130 larvae and pupae/100 plants. A braconid parasitoid heavily attacked larval populations and a pathogen, *Nosema invadens* or nr., infected all stages in the field in Argentina. *Sameodes albiguttalis* would probably be an effective control agent if released in regions where it is not native. A synergistic effect between it and weevils of the genus *Neochetina* is predicted. The factors affecting its potential effectiveness are discussed.

Waterhyacinth, *Eichhornia crassipes* (Mart.) Solms, probably orginated in tropical South America, but man has taken it into most tropical and subtropical areas of the world as an ornamental. There it has escaped cultivation to become the most damaging aquatic weed in the world. The literature on the organisms known to attack waterhyacinth and the progress of research on biological control has been reviewed by Bennett (1967, 1973, 1974, 1977), Coulson (1971), Perkins (1972, 1973b), Zettler and Freeman (1972), Andres and Bennett (1975), Center (1975), and Freeman et al. (1975).

Waterhyacinth is attacked in the U.S. by larvae of the native moth, *Arzama densa* (Walker), that normally feeds on the closely related pickerel-weed (*Pontederia cordata* L.) that is native in the U.S. (Vogel and Oliver 1969a, b). In addition, the mite, *Orthogalumna terebrantis* Wallwork, apparently has been accidently introduced from South America and attacks the plant over much of its range in the U.S. (Bennett 1970, Gordon and Coulson 1974, Cordo and DeLoach 1975, 1976). Waterhyacinth is also attacked by certain plant pathogens in Florida (Freeman et al. 1975). However, these organisms provide but little control of waterhyacinth under natural conditions. Waterhyacinth is also heavily fed on by the native manatee (*Trichechus manatus* L.) and in laboratory tests by the introduced white amur fish (*Ctenopharyngodon idella* Valenciennes) (Andres and Bennett 1975), but both of these organisms are rather indiscriminate feeders and numbers sufficient to control waterhyacinth probably would also greatly reduce other aquatic vegetation.

Explorations to find more effective biological control agents for waterhyacinth in South America were made by Vogt (1960, 1961), Silveira-Guido,[5] Bennett and Zwölfer (1968), Bennett (1970), and since 1967 by B. D. Perkins[6] and the authors from this laboratory.

Research has been underway at Hurlingham, Argentina, since 1967 to test and introduce insects into the United States for biological control that would be both effective and that would attack only waterhyacinth (DeLoach 1975a, b 1976, DeLoach and Cordo 1976a, b, Cordo and DeLoach 1975, 1976, Perkins and Maddox 1976, Silveira-Guido and Perkins 1975). As a result, 2 species of weevils, *Neochetina bruchi* Hustache and *N. eichorniae* Warner, now have been introduced and released in Florida (Perkins 1973a). Both appear to be reducing stands of waterhyacinth but their dispersal into other areas is relatively slow Perkins,[6] (pers. comm.). Although the weevils were the 1st species introduced, DeLoach (1975a) rated the moth *Acigona infusella* Walker as potentially the most effective biological control agent for waterhyacinth; however, it may have too wide a host range to permit introduction. He rated the pyralid moth *Sameodes* (="*Epigagis*")

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[5] Silveira-Guido, A. 1965. Natural enemies of weed plants. Final report. Unpubl. report, Dept. Sanidad Vegetal, Univ. de la Republica, Montevideo, Uruguay. 128 pp.

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albiguttalis (Warren) as the 2nd most potentially effective control agent.

Silveira-Guido[5] in Uruguay conducted the 1st biological observations of *S. albiguttalis* and found that the larvae tunnel in the petioles and pupate in a silken cocoon in the bulbous part of the petiole. Rao[7] in India, by using a culture reared from pupae imported from Trinidad, reported that the eggs hatched in 5–11 days, larvae developed in 12–41 days in different months of the year, and pupae required 6–12 days for development. Although his studies were severely limited by disease in the culture, disease-free females laid a maximum of 216 eggs and he reared 8 generations in the laboratory in 9 mo and 11 days.

Cordo and DeLoach (1978) studied the host specificity of *S. albiguttalis* extensively and reported that it was safe to introduce into the United States. The following research was done during that study, at Hurlingham, Argentina, from 1973–77 to determine the life history of *S. albiguttalis*, its ecology in the field, and to estimate its potential effectiveness in reducing stands of waterhyacinth if introduced into the United States.

Taxonomy and Distribution

Sameodes albiguttalis was described by Warren (1889) as *Epichronistis* (?) *albiguttalis* from 3 ♀ collected in 1874 by J. H. W. Trail from the Rio Purus in the Amazon basin. Hampson (1899) listed it in the genus *Pyrausta* Schrank. The species was subsequently transferred in the collections of the British Museum (Natural History) and the U.S. National Museum to *Sameodes* Snellen, which Hampson (1918) sank as a synonym of *Epipagis* Hübner. However, as Pastrana[8] (pers. comm.) points out, Hampson did not publish the species transfer. The combination *Sameodes albiguttalis* (Warren) appears to have been published first by Biezanko et al. (1957), who listed the species from Uruguay, and the combination *Epipagis albiguttalis* (Warren) by Bennett and Zwölfer (1968). The latter name is used in the unpublished reports of Silveira-Guido,[5] Rao,[7] and of this laboratory.

Munroe[9] (pers. comm.) states that the taxonomy is complicated by both nomenclatorial confusion and incompletely resolved mistakes and uncertainties in the generic classification. He believes that *albiguttalis* probably belongs to an unnamed genus and not to either *Sameodes* or *Epipagis*. As noted by Munroe (1950), the type-species of *Sameodes* is the Old World tropical species *Sameodes trithyralis* Snellen, a synonym of *S. cancellalis* (Zeller). Though in his 1950 paper he left a number of North American species in *Sameodes*, Munroe now feels that some of these should be referred to *Diacme* Warren, type-species *Samea phyllisalis* Walker, and the rest to *Mimorista* Warren, type-species *Samea botydalis* Guenée.

Munroe (1955) showed that the name *Epipagis* properly applies to the species previously placed in North American lists in *Stenophyes* Lederer, a genus incorrectly synonymized by Hampson (1899) with the unrelated *Crocidophora* Lederer. Though the species of *Epipagis* as thus interpreted are related in a general way to *Sameodes*, they have never been included in that genus even in its broad sense, and they had not been placed in *Epipagis* prior to Munroe's paper, except for Hübner's inclusion of the type-species when he established *Epipagis*. Munroe included 3 North American species in *Epipagis*: the southeastern *E. huronalis* (Guenée); *E. forsythae* Munroe, described from Florida, but now known also from the West Indies; and *E. disparilis* (Dyar), from the southwestern United States and Mexico. These 3 species are very closely related, and at least 2 more also closely related species occur in tropical America, completing our present knowledge of the genus. The life histories appear to be unknown, but there is no indication that the species are associated with aquatic plants or aquatic habitats. The genus is related to *Diacme* and *Mimorista* (see above), whose life histories also seem to be unknown. All 3 genera are related to the holarctic genus *Mecyna* Doubleday, whose larvae feed on terrestrial plants.[9]

The type-species of *Sameodes*, *S. cancellalis* (see above), is common in weedy places over most of the Old World tropics. Its habits do not suggest that it has an aquatic food plant. Several closely related species of *Sameodes* occur in different parts of Asia. *Samea ecclesialis* Guenée, the type-species of *Samea* Guenée, is closely similar in structure and habits to *Sameodes cancellalis*, and occupies comparable habitats in the tropics and subtropics of the New World. The life history is poorly known but the U.S. National Museum has larvae from "an unknown weed," presumably terrestrial. *Samea ecclesialis* has a few close relatives in the Neotropics; these species may have similar life histories.[9] However, another less closely related species at present placed in *Samea*, namely *S. multiplicalis* (Guenée), is known to feed on *Salvinia*, *Pistia*, and other aquatic plants, including waterhyacinth under some conditions (Bennett 1966, 1970, Bennett and Zwölfer 1968, DeLoach unpublished data). *Samea multiplicalis* is abundant in Florida and widespread in tropical America. *Samea nicaeusalis* Walker and *S. alophalis* Hampson are neotropical species that closely resemble *S. multiplicalis* and which might be expected to have similar life histories. The genus *Somatania* Möschler, with a single known species, *S. pellucidalis* Möschler, recorded from Florida (Kimball 1965) and widely distributed in tropical America, is related and seems to be associated with aquatic habitats.[9]

Reference in current or past literature of species to such nominal genera as *Samea*, *Sameodes*, *Epi-*

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[7] Rao, V. P. 1972. Studies on four species of natural enemies for biological control of *Eichhornia crassipes*. Unpubl. Rept., Indian Station, CIBC, Bangalore, India. 15 pp.

[8] Ing. Agron. José A. Pastrana, Inst. Patología Vegetal, Centro Nacional de Investigaciones Agropecuarias, INTA, Villa Udaondo, Buenos Aires Prov., Argentina (pers. comm.).

[9] Eugene G. Munroe, Biosystematics Research Institute, Agriculture Canada, Ottawa (pers. comm.).

pagis, Diacme, and *Mimorista* should not in general be taken to indicate a probable aquatic host association. The life histories of most of the species that really belong to these genera are unknown, but it seems likely that many if not most of them will prove to be terrestrial. Also, many of the species are grossly misclassified and will in time be transferred to other genera or even subfamilies. For example, the species group that includes "*Epipagis*", "*Chrysobotys*" or "*Sameodes*" *cambogialis* (Guenée), *Loxomorpha citrinalis* Amsel (not to be confused with "*Sameodes*" *citrinalis* Hampson), "*Mimorista*" *flavidissimalis* (Grote) and "*Mimorista*" *pulchellalis* (Dyar), as well as "*Mimorista* sp." of Costa Lima and of Mann, has been recorded as feeding on cacti and (somewhat questionably) on other terrestrial plants (Costa Lima 1968, Mann 1969, Pastrana[8] pers. comm.). However, this group belongs to a separate genus not very closely related to *Samea, Sameodes, Epipagis,* or *Mimorista.*[9]

Pending completion of his current studies, Munroe[9] recommends that *albiguttalis* be placed provisionally in *Sameodes,* as we have done in the present paper.

Sameodes albiguttalis appears to be distributed throughout tropical and subtropical South America. Silveira-Guido[5] collected it from waterhyacinth in Uruguay and at Iguazu (on the border between Argentina and Brazil), Bennett and Zwölfer (1968) collected it regularly from waterhyacinth in Trinidad, Guyana, Surinam, and the Amazon basin of Brazil, and during the present study we collected it near Buenos Aires, Argentina.

Methods

The population density of *S. albiguttalis* on waterhyacinth was sampled during 3 yr in a small canal ca. 7 m wide near the Río Paraná at the town of Dique Luján, 40 km NW of Buenos Aires, and at a site called "new canal" 2 km N of the small canal. Also, samples were taken at 2 sites at Campana 70 km NW of Buenos Aires: at the inlet 1 km downstream from the Balneario Municipal, and at a lagoon of ca. 3 ha across the Río Paraná from the Balneario; these locations are at ca. 34° 15′ S latitude. When populations became highly diseased in 1976, an isolated population that appeared to be disease-free (i.e., normal fecundity, survival of adults and eggs, and no microsporidian spores found in the adults) was found at Dique Los Sauces at La Rioja, 1000 km NW of Buenos Aires. According to the local water management authorities at Dique Los Sauces, waterhyacinth is not native there but was introduced into the lake since 1947.

Two methods were used to sample population density. At the Campana lagoon, all the petioles were examined ca. every 2 wk in either 4 or 8 sampling units of ¼ m^2 at random locations within the stand of plants. At the Campana inlet and at Dique Luján, larger samples of several hundred plants were examined at irregular intervals. In both cases, the petioles were dissected, and larvae and pupae of *S. albiguttalis* were removed and placed with petioles in jars for transport to the laboratory and subsequent rearing.

Eggs and larvae used in the life history tests were reared from larvae and pupae dissected from the petioles of waterhyacinth in the field. Each morning the adults that had emerged in ½-liter paper cartons were transferred to 2-liter, screen-topped glass jars containing leaves of waterhyacinth plants; sometimes adults were allowed to emerge from pupae in the jars with the plants. Ovipositional sites were made available by breaking the pseudolamina between the veins near the petiole, by cutting off slices or cutting notches in the petiole, and by using leaves with feeding lesions of weevils of the genus *Neochetina* or of snails. All these methods exposed the spongy aerenchyma cells that moths preferred for oviposition. Females mated and oviposited readily in the jars or in 1-m^3 screen cages. Moths were provided with a 1:3 honey-water solution in sponges hung from the tops of the cages as a standard rearing procedure, but we did not determine if they actually fed. The jars were held in a temperature cabinet at 25°±2°C and a 16-h photophase from ten 40-w Gro-lux® fluorescent tubes.

We did not attempt to transfer eggs to other plants after they were laid, but the newly hatched larvae were easily transferred with a small brush to punctures made in the petioles of other plants. Plants for use in tests were collected from a stand of waterhyacinth in the Río Reconquista near Hurlingham that was not infested by *S. albiguttalis* or *Neochetina* weevils. This stand was isolated by at least 15 km from any other known stand of waterhyacinth. Plants used during larval development tests or predation tests were held in hydroponic solution (described by DeLoach 1976) in 2-liter containers or in small glass aquaria 36×28×35 cm with a screen top.

Tests to measure fecundity, preference for ovipositional site, duration and survival of eggs, larvae, and pupae, and the rate of increase were all made in the 25°C temperature cabinet; other tests were made at room temperature in the laboratory or in the greenhouse.

Our specimens of *S. albiguttalis* were first identified by Pastrana[8] and later confirmed by Ferguson[10] and Munroe.[9] Voucher specimens of the insects from these studies were deposited in museums of the USDA, Beltsville, MD, the Biosystematic Research Institute, Ottawa, and the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires.

Results

Adult

Adult *S. albiguttalis* are yellowish tan with brown markings (Fig. 1). Females are darker, especially on the forewings, than the males; the tip of the female abdomen is tube-shaped and that of the male

[10] Douglas C. Ferguson, Systematic Entomology Laboratory, Agric. Res. Serv., USDA, Beltsville, MD.

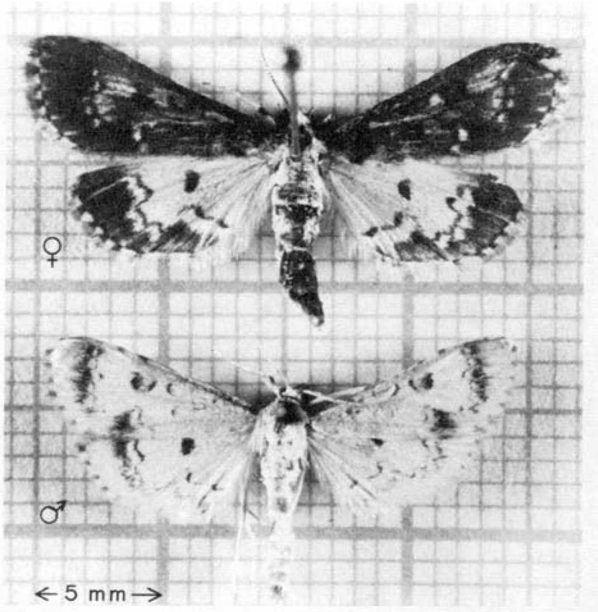

FIG. 1.—Adult female and male of *Sameodes albiguttalis.*

has claspers that terminate in a sharp point. Females had a wingspan of 22.7 mm (range of 10 = 20.0–24.7) and a body length of 10.1 mm (range of 10 = 9.5–11.0); males had a wingspan of 19.7 mm (range of 10 = 17.0–22.3) and a body length of 9.3 mm (range of 10 = 8.0–10.5).

Females in the laboratory laid an average of 301.5 eggs each (SD = 140, range = 112–592 for 19 ♀) during their life, 70% of them during the 2nd and 3rd nights after the females emerged and 94% the 1st 4 nights. Females lived an avg of 5.7 days and the maximum was 9 days (Table 1).

Females usually laid their eggs in the exposed, spongy air-filled aerenchyma cells in injured areas of the waterhyacinth leaves where the epidermis had been removed by the feeding of weevils of the genus *Neochetina,* by snails, or by other causes; one egg fit snugly in each cell (Fig. 2A). Females also laid readily in areas where we had removed the epidermis with a knife or in cuts made in the leaf or petiole and in the cut ends of petioles. Less often they oviposited on undamaged plants.

Eggs were usually laid singly in the laboratory, but groups of eggs in several adjacent cells were also seen. Of 983 eggs examined that were laid in the laboratory, 35.7% occurred singly, 16.5% in groups of 2, 13.7% in groups of 3, 11.8% in groups of 4, 4.1% in groups of 5, and lesser numbers in groups of 6–20 eggs each.

In one test, we compared the preference of moths for ovipositing in feeding spots of *Neochetina,* in cuts made with a knife, or in undamaged waterhyacinth plants. In each replication, 1 ♀ and 1 ♂ moth (emerged the previous night) were placed with a small plant of each of the 3 types in separate 2-liter glass jars and held in the 25°C cabinet; 4 replications were made. Eggs were counted and plants changed daily until all moths died. Twice as many eggs were laid on plants with both feeding spots and cuts as on plants with feeding spots only, and only a few were laid on undamaged plants; differences between the 3 treatments were significant at the 95% level (Table 2). On the undamaged plants, females placed 70 eggs in the narrow space between the central petiole and the apical part of the bract covering it, 27 on the surface of the pseudolamina, and 3 on creases in the pseudolamina; 22 were placed in *Neochetina* oviposition punctures and 12 in a feeding spot unnoticed when the plant was placed in the jar.

Another test measured the time of day when females oviposited. Waterhyacinth plants were ex-

Table 1.—Fecundity and survival of adult *Sameodes albiguttalis* and viability of eggs.

Age of females (days)	No. females surviving	Survival (l_x)	Eggs laid: No.	Eggs laid: % of total	Eggs/♀/day (m_x)	l_xm_x	Viability of eggs[a]: No.	Viability of eggs[a]: % hatch
1	19	0.499	1641	28.6	86.4	43.1	1421	84.4
2	19	.499	2399	41.8	126.3	63.0	849	98.2
3	19	.499	678	11.8	35.7	17.8	180	86.1
4	19	.499	659	11.5	34.7	17.3	349	94.0
5	13	.341	306	5.3	23.5	8.0	120	74.2
6	10	.263	27	0.5	2.7	0.7	16	50.0
7	6	.158	28	0.5	4.7	0.7	12	100.0
3	3	.079	0	0	0	0	0	
9	1	.026	0	0	0	0	0	
10	0	.000	0				0	
Total			5738			150.6[b]	2947	
Mean			302.0					89.1

[a] Includes only the 2947 eggs laid by 11♀ from La Rioja; data were not taken on percent hatch of the other eggs.
[b] Net rate of increase, R_0 = times increase per generation.

posed to 22 ♀, 28 ♂, and 8 moths of undetermined sex in a 0.7-m^3 screen cage in the greenhouse in early December (sunset was at ca. 7:00 p.m.). The plants were changed and the eggs were counted periodically for 3 days. Females laid 84% of their eggs between 7 and 11 p.m. Results were as follows:

Hour of day	No. eggs laid
5–7 p.m.	15
7–9 p.m.	47
9–11 p.m.	81
11 p.m.–8 a.m.	10
8 a.m.–5 p.m.	0

Egg

The eggs of *S. albiguttalis* are creamy white, without obvious markings, ovoid, and 0.47 mm (0.40–0.53) long by 0.37 mm (0.33–0.40) diam. Duration of the egg stage was measured for 1109 eggs held at 24°±1.6°C. The eggs were laid by adults held at 24°C and dissected from the plants the morning after oviposition. The eggs were surface sterilized by placing a drop of 0.05% sodium hypochlorite on them without subsequent rinsing; then they were held on wet filter paper in petri dishes and examined once a day for hatching. All eggs had hatched when examined on the 5th or sometimes the 4th day after oviposition but we assume that they had hatched the night before, i.e., at a time halfway from the previous examination the afternoon before. Duration of the egg stage was thus 3–4 days.

Viability was 89.1% for 2947 eggs laid by 11 ♀ reared from pupae collected at La Rioja (Table 1). Of the total of 322 eggs that did not hatch, 202 were from 1 ♀ that apparently did not mate the 1st night; if these are excluded, 95.6% of the eggs hatched.

Larva

Newly hatched larvae fed just below the epidermis of the petioles and the feeding damage could be

Table 2.—Oviposition by *Sameodes albiguttalis* in wounded and undamaged waterhyacinth plants.

Rep. no.	No. eggs laid on indicated type of plant[a]: With *Neochetina* feeding lesions	With *Neochetina* feeding lesions plus cuts	Undamaged
1	177	283	80
2	289	505	26
3	116	299	28
4	138	46	—
Total	720	1554	134
Mean eggs/♀	180	388.5	44.7

[a] Differences between all 3 treatments were significant at the 5% level according to Duncan's multiple range test.

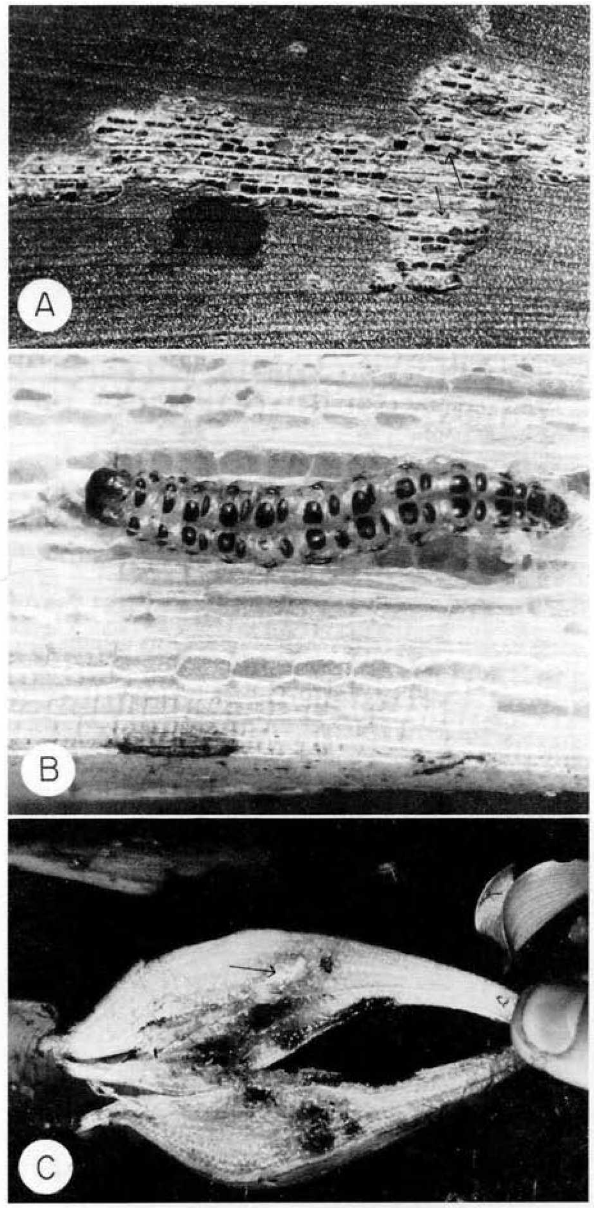

Fig. 2.—Immature stages of *Sameodes albiguttalis*: A) Eggs laid in exposed cells of a waterhyacinth leaf in the feeding lesion of a snail (ca. 40 eggs present), B) Full-grown larva in its feeding tunnel in the petiole (larva = 19 mm long), C) Cocoon in the bulbous petiole of waterhyacinth.

seen 1–2 days after hatching. Larvae from eggs laid on the pseudolamina tunneled within for 1–2 days and then apparently exited, crawled down the narrow part of the petiole, and entered again in the globose part of the petiole where they continued feeding (Fig. 2B). They appeared to feed singly, although several small larvae might feed in one petiole, and no gregarious habits were observed. In the field we usually found only one large larva/plant.

Full-grown larvae usually selected a pupation site

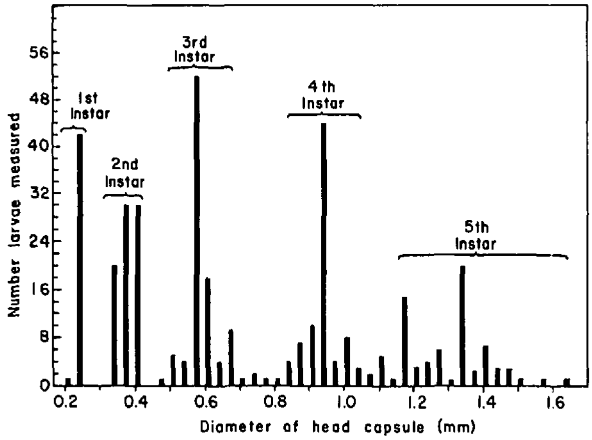

FIG. 3.—Frequency distribution showing number of larval instars of *Sameodes albiguttalis*.

in the mid-part of a globose petiole that had little prior feeding. The full-grown larva hollowed out a pocket, cut a round exit hole below it, tied the plug of plant epidermis from the exit hole in place with silk, and lined the exit tunnel with silk. The larva spun a white cocoon and pupated (Fig. 2C). Full-grown larvae reared in the laboratory from field-collected larvae averaged 18.7 mm long (range = 16–21 for 18 larvae). Dry weight of full-grown larvae was 6.61 mg (mean of 25 larvae dried at 110°–120°C).

Head capsule measurements of 377 larvae indicated the presence of 5 larval instars (Fig. 3). All 5th-instar larvae with head capsules 1.17 mm diam or less (Fig. 3) were reared in petri dishes, and many died before pupating. Head capsules of larvae that were spinning their cocoons were always larger than 1.33 mm, and those of larvae on plants in the greenhouse averaged 1.43 mm diam. The ratio between the median of each succeeding instar varied only from 1.43–1.65×. However, individual larvae that were measured were selected from a mass culture rather than by following each larva through all stages, so an actual count of instars was not obtained.

Each instar required 3–4 days for development, except the 5th instar that required 7 days, and the entire larval period required ca. 21 days in the laboratory at 25°C (Table 3).

Survival of larvae was measured in the greenhouse at 26°±9°C by placing 3 eggs in each of 4 plants in small aquaria (30×37×35 cm) and counting the pupae 26 days later; 4 replications were made. A total of 25 pupae were recovered from the original 48 eggs.

If we calculate that 2 of the eggs would have failed to hatch (egg survival was 95.6% in previous calculations), then 46 larvae would have emerged from the 48 eggs. From these 46 larvae, 25 pupae were produced. Thus, survival during the larval stage theoretically was 54.3%.

Table 3.—Developmental time and survival of each life stage of *Sameodes albiguttalis* at 24°C in the laboratory.

Stage	Mean width head capsule (mm)	Mean duration (days)		% survival	
				Each stage	Cumulative
Egg			4	95.6	95.6
Larva					
1st	0.23	3			
2nd	0.40	4			
3rd	0.57	3			
4th	0.93	4			
5th	1.33	7			
Total			21	54.3	51.9
Pupa			7	96.0	49.8
Adult to peak oviposition			2		
Total generation			34		

Pupa

Pupae of *S. albiguttalis* averaged 11.0 mm long (range = 10.0–12.1) and 2.85 mm wide (range = 2.5–3.1) for 5 ♂ and 5 ♀ measured; little difference was noted in the sizes of males and females. Females could be distinguished from males by the following characters (Fig. 4):

Character	♂	♀
genital opening (GO)	9th seg	8th & 9th seg
posterior margin of 8th seg	not divided by GO	divided by GO
rounded pads on each side of GO	present	absent
antennae	reach posterior margin of wing pad	terminate before posterior margin of wing pad

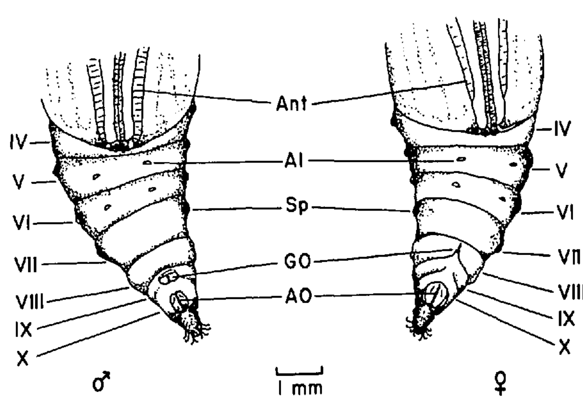

FIG. 4.—Pupae of *Sameodes albiguttalis* showing characters used to distinguish the sexes. Ant—antenna, Al—alveoli, Sp—spiracle, GO—genital opening, AO—anal opening, IV–X—abdominal segments.

From the test on larval survival, one pupa died and 24 healthy adults emerged from the 25 pupae recovered, a survival rate of 96.0% for the pupal stage. Only one pupa was found in each of 23 petioles and 2 were found in one petiole; the pupae were located in the bulbous petioles as previously observed in the field.

Generation Time and Rate of Increase

In the laboratory at 25°C, a complete generation required 34 days: 4 days for the egg stage, 21 days for the larval stage, 7 days for the pupal stage, and 2 days before the adult reached peak oviposition (Table 3).

The rate of increase at a density of 3 eggs/plant was calculated according to the method of Birch (1948) by using age-specific survival and fecundity calculated from the previous life history data (Fig. 5). The net rate of increase (times increase per generation, R_0) was 150.6, the intrinsic rate of increase (r_m) was 0.14675, and the generation time (T) was 34.17 days. Thus, the finite rate of increase (or number of times the population would increase per day = $\text{antilog}_e r_m$) was 1.158, and 4.72 days would be required for the population to double (days to double = $\log_e 2/r_m$).

We should emphasize that this calculation of the rate of increase is valid only at an original density of 3 eggs/plant on rather small plants. Density of the eggs, and subsequent degree of competition between larvae and possible cannibalism by larvae, may be of great importance in larval mortality. Although we never observed cannibalism, the 50% larval mortality in these tests is difficult to explain unless some intraspecific competition or disease were involved. The eggs and larvae were taken from cultures believed to be pathogen free, but the microsporidian is difficult to detect and its presence cannot be ruled out; if present, the incidence of disease might also increase with density. Thus, the rate of increase might be higher than calculated at lower larval densities and much lower at higher larval densities.

Seasonal Abundance

Populations in the field varied greatly from year to year and between locations in the same year. In 6 yr of observations at several locations in Argentina, populations large enough to cause heavy damage to waterhyacinth were found in only 4 instances: in 1973–74 in the small canal at Dique Luján; in 1975–76 at the Campana inlet, at the new canal, and at the small canal at Dique Luján (Fig. 6). In addition, populations reached 128 larvae and pupae/100 plants at the small canal at Dique Luján in Jan. 1977. The occurrence of generation peaks in the field is based mostly on data from 1976. Counts made during the 1973–74 and 1974–75 seasons generally confirmed these findings, but populations were too low in those years for reliable measurements of generations.

Sameodes albiguttalis appeared to have 5 generations in the field at Dique Luján (Fig. 6). Generation peaks were in mid-Nov., Jan. 7 (49 days), Feb. 6 (30 days), and Mar. 18 (41 days). A 5th generation of larvae appeared ca. June 16 (90 days). The 5th generation occurred in May 1975 but in 1976 it was delayed until June by cool weather. Larvae of the 5th generation, and probably some from the 4th generation, overwintered in the petioles of waterhyacinth. No pupae of the 4th generation were found in the field after June 16. Larvae of the 5th (overwintering) generation began pupating in Sept. (Fig. 6).

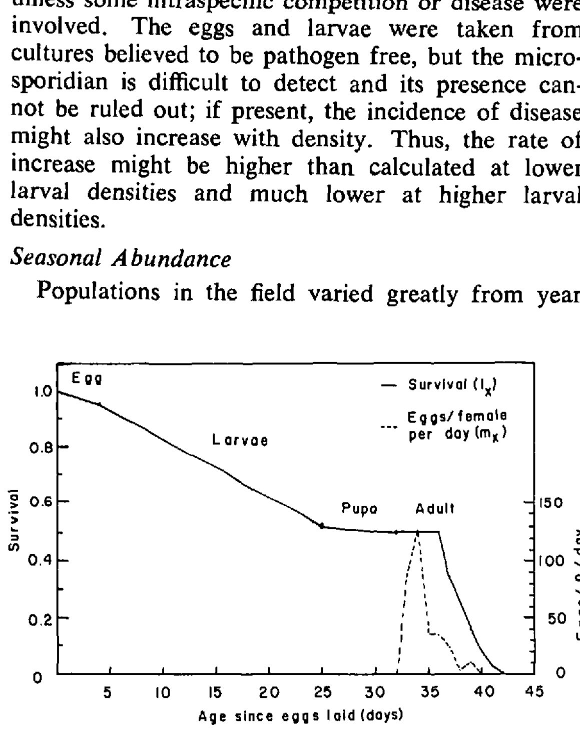

FIG. 5.—Survival (at an initial density of 3 eggs/plant) and oviposition of *Sameodes albiguttalis* at 25°C.

Damage Caused to Waterhyacinth

The larvae of *S. albiguttalis* damaged waterhyacinth by feeding inside the petioles and the bud but they usually did not enter the plant crown. This feeding caused the petioles to break and die and killed the growing bud (Fig. 7). The large larvae sometimes moved to other petioles or to other plants and might bore through several petioles just before pupating. We found no evidence that the larvae were vectors of primary plant pathogens but the feeding did provide entry sites for invasion by facultative or saprophytic microorganisms that caused decay. The larvae damaged plants throughout the growing season but reached a peak in mid-summer. In heavy infestations, the plants did not recover before fall and suffered heavy die-back during the winter.

Damage done by *S. albiguttalis* to stands of waterhyacinth in nature was observed during 3 growing seasons in the small canal at Dique Luján and at Campana. A small population of 12 larvae/100 plants was found in the 1st generation in Nov. 1973. The population increased in the 2nd generation, in Jan. 1974, to 28 larvae or pupae/100 plants. Those larvae severely damaged or destroyed the central part of the bud of most plants and 12% of all petioles sampled were damaged. This damage, combined with heavy damage done by the weevils *Neochetina bruchi* and *N. eichhorniae*, greatly reduced the stand of waterhyacinth to the point that by Aug. (mid-winter), the stand was estimated to cover only ⅛ the area occupied the previous Jan. Stands are always reduced by cold weather during

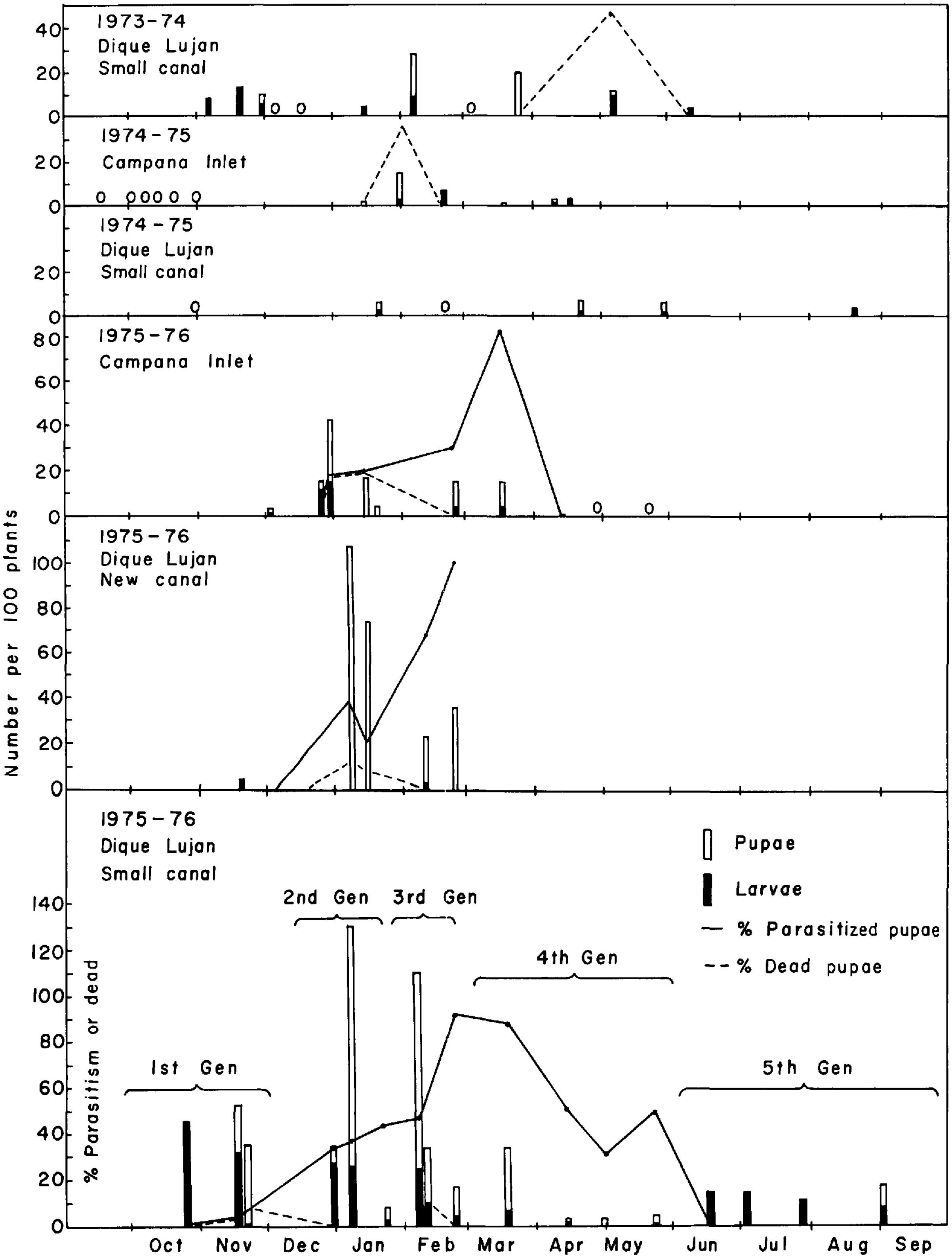

FIG. 6.—Seasonal abundance of *Sameodes albiguttalis* determined from periodic field samples taken during 3 yr (% dead or parasitized may be read from the ordinate scale, i.e., 60 = 60 larvae/100 plants or 60% parasitized; % is based on number of prepupae or pupae inside cocoons on each date, not including other larvae in the sample).

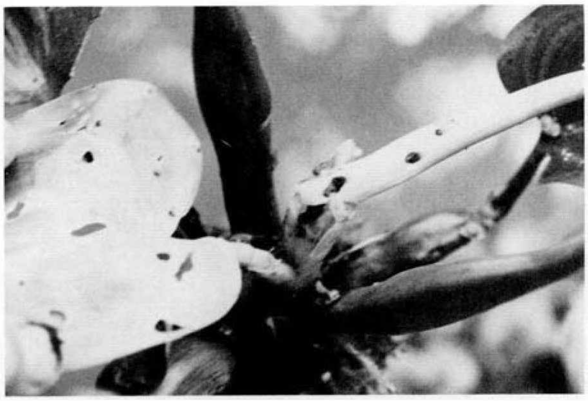

FIG. 7.—Typical damage to bud of a waterhyacinth plant caused by larvae of *Sameodes albiguttalis*.

the winter but that in the small canal was reduced much more than in nearby areas exposed to similar weather conditions.

Throughout the next growing season (Nov. 1974–May 1975), the stand remained small, and the population of *S. albiguttalis* remained low; anchored waterhyacinth, *Eichhornia azurea* (Swartz) Kunth, replaced waterhyacinth as the dominant plant. Maximum populations on waterhyacinth that season were 6 larvae and pupae/100 plants in the 3rd generation and 7/100 plants in the 4th generation (Fig. 6).

By the spring of the 3rd season of observations (Nov. 1975), the stand of waterhyacinth was again increasing but did not reach the abundance seen during 1973–74. Nevertheless, populations of *Sameodes* larvae and pupae reached the highest levels seen—130/100 plants in the 2nd generation and 110/100 plants in the 3rd generation (Fig. 6). Populations in the "new canal" at Dique Luján (ca. 2 km NW of the "small canal") also were very high, reaching 107/100 plants in the 2nd generation.

At Campana and the other areas sampled, populations of *S. albiguttalis* were generally much lower than at Dique Luján. In th 1973–74 season, a maximum of 4 larvae and pupae/100 plants was found in the lagoon at Campana, and in 1974–75 a maximum of 15/100 plants was found in the inlet at Campana. In 1975–76 a maximum of 42 in the 2nd generation and 15 in the 3rd generation/100 plants were found in the inlet at Campana; only a few samples were taken in the lagoon during 1975–76 and the maximum was 4/100 plants in the 2nd generation.

The large population of *S. albiguttalis* in the 1973–74 season and the heavy damage it did apparently occurred because rates of parasitism (6.0%) and disease (7.7%) were low during the 2nd generation in Jan. In the 1975–76 season, parasitism in the 2nd generation was much higher (35%), and it increased through the 3rd generation. This probably explains the population decline in the 4th and 5th generations. (Disease was also high but was not measured.)

Competition with Acigona

The larvae of both *S. albiguttalis* and *Acigona infusella* feed inside the petioles of waterhyacinth, and both are capable of causing heavy damage to the plant. The 2 species have similar life histories and behavior on waterhyacinth, but they seem to prefer different parts of the plant and therefore are ecologically separated. Several attempts were made to measure this separation, but sufficient populations of both species to make comparisons meaningful were present only in the inlet at Campana on Apr. 11 and 18, 1975. On both dates, *Acigona* strongly preferred the tall slender plants (ca. 80 cm high) and *Sameodes* preferred plants with globose leaves (ca. 25 cm high) (Table 4). However, this difference was not conclusive because of the small number of samples.

Natural Enemies

Sameodes albiguttalis is heavily attacked in the field in Argentina by a parasitoid, a pathogen, and possible by predators. The solitary braconid, *Hypomicrogaster* n. sp.[11] that emerged from the full-grown larva inside the host cocoon was the most abundant parasitoid. The rate of parasitism increased in 1975–76 from near zero in the 1st generation to 35% in the 2nd, to 50% in the 3rd, and to 90% in the 4th in the small canal at Dique Luján (Fig. 6). Less complete season-long data were obtained at other locations, but the results were generally similar if moderate to large populations of host larvae were present. In 1975–76, parasitism at the new canal at Dique Luján reached 38% in the 2nd generation and 100% in the 3rd generation; at the Campana inlet it reached 83% in Mar. (Fig. 6). Populations of *S. albiguttalis* were low during the spring of 1976–77 at the small canal at Dique Luján, and parasitism was only 4% on Jan. 4, 1977; by Jan. 28, populations had increased to 128 larvae + pupae/100 plants, and parasitism was 44.4%. Percent parasitism and disease was based on the number of prepupae or pupae inside the cocoons on each date, not including smaller larvae in the sample.

A 2nd braconid parasitoid was determined by Marsh,[12] as *Agathis* sp. It also pupated inside the

[11] Being described by Dr. Luis DeSantis, La Plata Univ., La Plata, Argentina.
[12] Paul M. Marsh, Systematic Entomology Laboratory, Agric. Res. Serv., USDA, Beltsville, MD.

Table 4.—Preference of *Sameodes albiguttalis* and *Acigona infusella* for different phenotypes of waterhyacinth in the field.

Type plant	No. of larvae and pupae collected/100 plants[a] *Sameodes*	*Acigona*
Short, globose	4.88	2.31
Tall, slender	0.00	28.51

[a] A total of 389 globose plants and 221 slender plants examined on 2 dates, Apr. 11 and 18, 1975, at the Campana inlet.

host cocoon. Adults were ca. 1 cm long (twice as long as *Hypomicrogaster*), and the female had an ovipositor ca. the length of the body. *Agathis* sp. was rare, and only 2 adults were reared during the studies.

A microsporidian pathogen was found by Allen[13] and identified by Maddox[14] as a *Nosema* species near *Nosema invadens* Kellen Lindegren, as determined by host range studies and ultrastructural features of the spores. The pathogen appeared to infect all stages of *S. albiguttalis;* it greatly reduced fecundity and longevity of adult moths, and infected females often died with the abdomen full of eggs. Fifteen females collected from a highly infected population in the inlet at Campana in Feb. 1976 lived an avg of only 3 days (range = 1–5), laid an avg of only 29.1 eggs (range = 0–149), and only 26.5% of these eggs hatched. Healthy moths lived an avg 5.7 days, laid an avg 302 eggs/♀, and 89.1% of the eggs hatched (Table 2). On several occasions, 10–12% of the pupae found in the field were dead, but mortality was probably much greater than this because dead larvae tend to disintegrate rapidly, and most of them were not found.

The 2 most common predaceous insects found throughout the growing season in stands of waterhyacinth were the coccinellid *Coleomegilla quadrifasciata* Schonherr and the staphalinid *Paederus* sp.; staphalinids were sometimes observed in the feeding tunnels inside the petioles. In petri dishes in the laboratory, 1 staphalinid adult ate all 6 eggs of *S. albiguttalis* and killed 2 of 4 newly hatched larvae in 4 days; 2 adult *Coleomegilla* ate all 7 eggs they were given in 1 day. These predators also were placed on waterhyacinth plants in aquaria where moths of *S. albiguttalis* were allowed to oviposit. The predators appeared to reduce the number of larvae of *S. albiguttalis* that were produced after 14 days by half of that in a control aquarium without predators. The tests were inconclusive because of insufficient replications and because the initial number of eggs laid was unknown, but they did indicate that predators might reduce populations of *S. albiguttalis* in nature.

Discussion and Conclusions

The moth, *Sameodes albiguttalis,* appears capable of giving good control of waterhyacinth if released in the United States. The tests of Cordo and DeLoach (1978) indicate that it is safe and will not damage beneficial plants. Our findings confirm the preliminary evaluation made by DeLoach (1975a) (based on the system developed by Harris 1973) that *S. albiguttalis* has the greatest effectiveness potential among the known insect candidates that are safe to introduce. It should complement the effectiveness of the 2 weevils, *Neochetina bruchi* and *N. eichhorniae,* already released in Florida. However, certain dangers to the insect exist that might limit its effectiveness after release.

Sameodes albiguttalis ranks high in potential effectiveness, compared with other candidate insects, for several reasons. The larvae attack the vital parts of the plant, the petioles and the bud, causing the leaves to die and break off and preventing growth of the bud. Although the plant can still reproduce from offshoots, these new plants may be attacked by the next generation of larvae. The tunneling inside the plant also allows the entry of secondary pathogenic organisms that cause decay. In Argentina, it appeared to cause heavy damage to waterhyacinth in the field, although the effect was confounded with damage from the *Neochetina* weevils. However, the damage was sporadic, apparently because of heavy attack by parasitoids and pathogens. Apparently *S. albiguttalis* could increase to a population sufficient to cause noticeable damage only in isolated stands where it could temporarily escape attack by these natural enemies.

The major factors limiting populations of *S. albiguttalis* in Argentina appear to be parasitoids and pathogens that probably are host specific. If these natural enemies can be eliminated in the "clean-up" procedure before release in the field in the U.S., *S. albiguttalis* should produce large populations in the fall that would cause much greater damage to waterhyacinth than seen in Argentina. Also, a larger overwintering population should result, producing a larger 1st generation and more damage in the spring.

S. albiguttalis attacks waterhyacinth throughout its known climatic range in South America, so presumably it would attack the plant throughout its range in the U.S., and in the rest of the world also. It attacks waterhyacinth throughout the growing season of the plant, although the spring buildup was somewhat slow and larval populations were reduced in the fall, probably because of parasitism and disease.

In order for *S. albiguttalis* to provide satisfactory control of waterhyacinth, it must overcome the enormous capacity for increase of the plant and its great capability to recover from damage. *Sameodes albiguttalis* seems capable of doing this. Although it does not produce a particularly large number of progeny per generation (which ranks low in Harris' (1973) scale), it produces several generations a year. The laboratory studies indicate that it has the capacity to increase 150 times in each generation of 34 days, or ca. 3 times that of the *Neochetina* weevils already released in Florida. Another advantage (not considered by Harris 1973) is that since it is a moth, and presumably a good flyer, it should disperse and find isolated stands of waterhyacinth more rapidly than the *Neochetina* weevils have done to date.

Sameodes albiguttalis does not rank high in some factors in Harris' (1973) system. In addition to its low number of progeny, the full-grown larvae are rather small and they show no tendency to feed gregariously; in fact, they may have some tendency toward cannibalism. The effects of possible cannibalism and other density-dependent factors are not yet

[13] George E. Allen, Dept. of Entomology and Nematology, Univ. of Florida, Gainesville, FL.
[14] Joe V. Maddox, Illinois Natural History Survey, Urbana.

well understood, and they might greatly reduce the rate of increase, especially at higher population densities. The effectiveness of *S. albiguttalis* as a biocontrol agent has not, of course, been demonstrated in another area of the world, since the present project will be the 1st introduction outside of its native range (it was studied in quarantine in India (Rao[7]) but not released in the field).

Sameodes albiguttalis is limited in host range to *E. crassipes* and it may rarely complete its life cycle on *E. azurea* (Cordo and DeLoach 1978). This habit ranks low in the system of Harris (1973), who postulates that oligophagous insects are more effective control agents than monophagous ones. The high degree of specificity does, however, make *S. albiguttalis* safe to beneficial plants, without which it could not be introduced at all.

Sameodes albiguttalis appears to be generally compatible with the weevils *Neochetina bruchi* and *N. eichhorniae* that have already been introduced. At Dique Luján in Argentina, a heavy attack by both *Sameodes* and *Neochetina* combined to nearly eliminate waterhyacinth in one year. *Sameodes albiguttalis* could supplement the control produced by *Neochetina* by attacking the growing bud, whereas *Neochetina* attacks the crown. However, the species may compete to some extent since both tunnel in the petioles.

A synergistic effect between *S. albiguttalis* and *Neochetina* is probable. Because *S. albiguttalis* prefers damaged leaf tissue for maximum oviposition (although some eggs were laid on undamaged plants), oviposition might be greatly increased if *Neochetina* were present to provide the feeding lesions. This effect probably was not critical in Argentina where the plants are much damaged by snails and other organisms, but in the U.S. where such damage is slight, the effect could be great.

Preliminary observations indicate that *S. albiguttalis* and *Acigona infusella* are compatible because they tend to attack different phenotypes of waterhyacinth plants; also, *S. albiguttalis* attacks the bud and *A. infusella* the plant crown. These results confirm the observations of Bennett and Zwölfer (1968). This difference in ecological niche may explain, together with the difference in host range (Cordo and DeLoach 1978), how the 2 species can coexist in the same area. *Acigona infusella* may compete with the *Neochetina* weevils since both feed in the plant crown. The introduction of *A. infusella* might give added control of waterhyacinth but our observations indicate that it would also damage the native pickerelweed (*Pontederia cordata*) that is considered of value as food for waterfowl in the U.S. (Cordo and DeLoach 1978). In countries where *P. cordata* does not grow, or is not considered a valuable plant, *A. infusella* would be a good candidate for introduction.

Sameodes albiguttalis will probably compete in the U.S. with the native *Arzama densa* since both attack similar parts of the plant; *A. densa* may loose out in this competition since waterhyacinth is not its natural host plant and *S. albiguttalis* presumably would be better adapted to it. The mite, *Orthogalumna terebrantis,* may also provide some competition for *S. albiguttalis* by making the leaves unattractive as oviposition sites, especially in mid-summer when the mite is most abundant (Cordo and DeLoach 1976).

The greatest risk to effective control in the U.S. is that *S. albiguttalis* might be attacked heavily by parasitoids or pathogens already present in the U.S. on other related insects in the same habitat (such as the native moth, *Arzama densa* on pickerelweed and waterhyacinth). Muesebeck et al. (1951) listed 27 species of *Microgaster* (= *Hypomicrogaster*) and 55 species of *Agathis* from North America, the same 2 genera that contained species attacking *S. albiguttalis* in Argentina. Bennett and Zwölfer (1968) reared 2 species of parasites from *S. albiguttalis* collected in Surinam and at Belem, Brazil, *Bracon* sp., a gregarious ectoparasite of the larvae, and *Spilochalcis* sp. from the pupae. Both of these parasitic genera are abundantly represented in the U.S. Also, a microsporidian, *Nosema* sp., attacks *A. densa* in Florida (Habeck and Allen 1974) that might be able to infect *S. albiguttalis* when released. The attack of general predators in the U.S. will probably reduce populations somewhat, since they also appear to attack eggs and larvae in Argentina, but the effect probably would be much less than that of specific parasites.

Another possible danger to future control in the U.S. is that the natural enemies of *S. albiguttalis* present within its native range in South America might move naturally into the U.S. through Central America and Mexico. Waterhyacinth occurs at several locations in Mexico but its distribution is not yet continuous to the U.S. *Sameodes albiguttalis* is not known to occur in Central America or Mexico but its introduction there would provide a nearly continuous bridge to the U.S. over which its natural enemies might eventually migrate. If this occurs, the control of waterhyacinth probably would be reduced substantially. One of the greatest advantages of *S. albiguttalis,* that of an exotic organism free of its natural enemies and free to increase possibly to the limit of its food supply, would then be lost.

Future research will attempt to measure the effectiveness of *S. albiguttalis* in controlling waterhyacinth after its release in the U.S. Of particular importance is the assessment of the factors that reduce its effectiveness, especially of any parasitoids or pathogens of other insects already in the U.S. that may attack it. Surveys will also determine if it damages any beneficial plants, especially pickerelweed.

If, after its release, *S. albiguttalis* proves ineffective in controlling waterhyacinth in the U.S., research could continue on the testing of other organisms in Argentina known to attack the plant, such as the moth *Acigona infusella* (Silveira-Guido 1971), the grasshopper *Cornops aquaticum* (Bruner) (Silveira-Guido and Perkins 1975), the scarab beetle *Chalepides luridus* (Burmeister) (Silviera-Guido),[8] the fly *Thripticus* sp. (Bennett and Zwölfer 1968), and the rust pathogen *Uredo eichhorniae* Fragoso and Ciferri (Freeman et al. 1975).[15]

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[15] *Sameodes albiguttalis* was released at 3 locations in the field in Florida on Sept. 22, 1977 by the U.S. Army Corps of Engineers (G. R. Buckingham, Biological Pest Control Research Unit, Agric. Res. Serv., USDA, Gainesville, FL, pers. comm.). Releases were also made in the field in Australia in Oct. 1977 (K. L. S. Harley, Division of Entomology, CSIRO, Long Pocket Laboratories, Indooroopilly, Queensland, Australia, pers. comm.).

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