Efficacy of Sameodes Albiguttalis as a Biocontrol of Waterhyacinth(U) Army Engineer Waterways Experiment Station Vicksburg MS Environmental Lab

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EFFICACY OF SAMEODES ALBIGUTTALIS AS A BIOCONTROL OF WATERHYACINTH

by

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Sameodes albiguttalis (Warren) is a South American pyralid moth species which was released in Florida in 1977 for the biological control of waterhyacinth. After it was determined that populations of this insect had become established in the field, various efficacy studies were begun. The first of these began in September 1978 and, ultimately, data were collected at 15 sites from throughout Florida. The objectives of these studies were to determine (a) if S. albiguttalis would be persistent, (b) if it could be augmented if it
20. ABSTRACT (Continued).

Were not persistent, and (c) if it had a significant impact upon waterhyacinth populations within the context of comparisons among other control agents and the plant's ability to recover from serious injury.

Data indicate that S. albiguttalis will, under certain conditions, be an effective biological control of waterhyacinth. This will generally be true only where the waterhyacinth population is in a predominantly colonizing mode. In these situations the plants are small, luxuriantly growing, have large, inflated leaf petioles, and often do not exist as part of a continuous mat. Infestations are usually heaviest along the developing fringe of a mat or in areas where the plants have been killed by frost, drought, or herbicide and are regrowing.

Life table studies of waterhyacinth leaves show distinct spatial patterns. Only S. albiguttalis larvae, weevil adults, weevil larvae, and occasionally environmental factors affect the young leaves, injure the apical buds of the shoots, cause leaf production to cease, and effectively kill the shoots. Most other factors usually only cause superficial injury and usually only to older leaves, although sporadic outbreaks of any of these agents may temporarily cause severe shoot injury. It is estimated that biological control by S. albiguttalis and the two species of waterhyacinth weevil results in an overall 34% reduction in waterhyacinth productivity. This is based upon the observed reduction to leaf longevity which is usually brought about by the early destruction of young leaves. Unfortunately, damage caused by S. albiguttalis larvae is sporadic.

Sameodes albiguttalis, more than either of the other two waterhyacinth insects (Neochetina eichhornea and N. bruchi), should fit comfortably into a management scheme. Its effectiveness may be maximized in a maintenance program where the waterhyacinth population is constantly perturbed and is always in a colonizing mode. Many possible management strategies exist in which this insect and herbicidal or mechanical control could be integrated and experimentation along these lines should be given a high future priority.
This report presents results of a biological control program being conducted for the Aquatic Plant Control Research Program (APCRP) by the U.S. Department of Agriculture (USDA), Science and Education Administration, Aquatic Plant Management Laboratory, Fort Lauderdale, Fla. The purpose of this program is to evaluate insects to determine their potential for use in aquatic plant control. This particular project in the overall program involved the efficacy of *Sameodes albiguttalis* as a biocontrol of waterhyacinth. Funds for this effort were provided by the Office, Chief of Engineers (OCE), under appropriation number 96X3122, Construction General, through the APCRP at the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. The principal OCE Technical Monitor for the APCRP was Mr. Dwight L. Quarles.

The principal investigator for the work was Dr. Ted. D. Center, USDA, who prepared this report.

The author would like to extend his appreciation to his technical staff, Mr. Willey C. Durden and Ms. Debra A. Corman, for invaluable aid throughout the project and to Ms. Beverly Benner for providing the excellent illustrations.

The research was monitored at WES by Mr. Edwin A. Theriot and Dr. Alfred F. Cofrancesco, Jr., of the Environmental Laboratory (EL) Wetland and Terrestrial Habitat Group (WTHG). The study was conducted under the general supervision of Dr. John Harrison, Chief, EL; Dr. Conrad J. Kirby, Chief, Environmental Resources Division; and the direct supervision of Dr. Hanley K. Smith, Acting Group Chief, WTHG. Mr. J. Lewis Decell was Manager, APCRP.

Commanders and Directors of WES during conduct of the study and preparation of this report were COL Nelson P. Conover, CE, and COL Tilford C. Creel, CE. Technical Director was Mr. F. R. Brown.

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* To obtain Celsius (C) temperature readings from Fahrenheit (F) readings, use the following formula: \( C = \frac{5}{9} (F - 32) \). To obtain Kelvin (K) readings, use \( K = \frac{5}{9} (F - 32) + 273.15 \).
EFFICACY OF SAMEODES ALBIGUTTALIS AS A BIOCONTROL OF WATERHYACINTH

INTRODUCTION

Waterhyacinth (*Eichhornia crassipes* (Mart.) Solms), a pernicious, floating, aquatic plant, possesses growth characteristics that make it an extremely efficient colonizer of the surfaces of open water bodies. Although easily killed by herbicides, only vigilant maintenance programs provide sustained control. Problems associated with herbicidal control include the public perception of a hazard associated with potentially toxic substances applied in water, the high cost of herbicides and the concomitant necessity of treating vast acreages, the alleviation of only a small proportion of the overall problem, and the expensive delivery systems and labor-intensive efforts necessary for use. Investigations begun in the late 1960’s led to the introduction of three species of insects into the U.S. in the hopes of providing some measure of biological control of waterhyacinth. Eradication was never a goal but it was hoped that these insect species would enhance management efforts and enable the control of a larger proportion of the problem.

Blackburn et al. (1969) and Andres and Bennett (1975) reviewed the early aspects of the biological control program. Bennett and Zwolfer (1968), Perkins (1974), and others surveyed for natural enemies of waterhyacinth in South America. Several scientists studied the host specificities and biologies of these insects and contributed a great deal to this project (Silveira-Guido and Perkins, 1975; DeLoach, 1976; DeLoach and Cordo, 1976 a,b, 1978; DeLoach et al., 1980; Cordo and DeLoach, 1978; Perkins and Maddox, 1976). This work led to the release of two species of weevils, *Neochetina eichhorniae* and *N. bruchi*, and the pyralid moth, *Sameodes albiguttalis*, in 1972, 1974, and 1977, respectively (Perkins and Maddox, 1976; Perkins 1973; Center and Durden, 1981; Center 1981b, 1982b).
In 1978, the U.S. Dept. Agriculture, Agricultural Research Service, and the U. S. Army Corps of Engineers, Aquatic Plant Control Research Program, undertook a cooperative project designed to study *S. albiguttalis*. This project was conducted in three phases: 1) release and establishment, 2) dispersal, and 3) effects on the target plant. The first two phases have been reported upon (Center 1981a, 1982a) and this report presents the results of the third phase.

Unless biocontrol agents dramatically impact the target plant, effects are not easily documented. This often leads to the erroneous conclusion that biological control does not work. Sub-lethal effects on the plant, however, contribute significantly to control, although these usually go unrecognized. Almost all studies of the effects of biological control agents on waterhyacinth focus narrowly on specific organisms and overlook potent interactions. In this study we investigate the effects of *S. albiguttalis* in the overall context of many factors which potentially interact to control, reduce, or otherwise impair waterhyacinth populations. With this in mind, we first review the biology of waterhyacinth and the pertinent information regarding its natural enemies. A knowledge of this information is important to understand the objectives of this project report.

**The Biology of Waterhyacinth**

Waterhyacinth seeds require warm, shallow water and high light intensities for germination. The submerged seedling roots in the substrate and subsequently forms four to five linear leaves (5 to 15 mm in length). The sixth and successive leaves have a great deal of aerenchyma tissue and, when sufficiently buoyant, the seedling breaks off from the rootstock and floats to the surface (for further details of germination and seedling formation, see Parija, 1930;
Robertson and Thein, 1932; and Penfound and Earle, 1948). Numerous fibrous, adventitious roots form on the stem (rhizome) at the base of the leaves and leaves continue to form at the apical bud in the center of the rosette. The general growth form of the shoot is monopodial, with the leaves being produced in a whorl. Branching is sympodial with ramets (vegetatively produced plants) formed from axillary buds (Figure 1,B) on stolons produced through the elongation of the internodes. As ramet production proceeds and crowding begins to occur, the newly formed leaves tend to become elongate rather than swollen or inflated (Figure 1,A). The inflated petiole leaf form (Figure 1,D) predominates at the edge of the mat nearest the open water or in populations where conditions preclude the development of a closed canopy. Leaf production occurs at a regular rate with the younger leaves in the center and the older leaves at the periphery of the rosette. The leaf consists of a thick petiole (2-3 cm in diameter), a narrow isthmus between the petiole and the blade, and a broad reniform to lanceolate lamina. The central leaves of the rosette are nearly vertical in orientation but the lateral leaves progressively bend outward by way of a reflexing at the leaf base. In the outermost leaves this bending orients the petiole at a very low angle and a second bend near the isthmus keeps the lamina in a more vertical position. The leaf persists for 5 to 6 weeks before it ultimately senesces. The leaves may become very large in crowded conditions, the petioles sometimes exceeding a meter in length (for a more detailed account of the morphology and anatomy of *E. crassipes* see Weber, 1950). Figure 1 illustrates the two growth forms with the structures labelled as mentioned in this text.

The habit of the plant is floating, erect with aerial leaves and submerged roots and rhizome. The high specific gravity of the submerged portion and the
Figure 1. The two generalized forms of waterhyacinth which are normally found in waterhyacinth communities. The small, "inflated-petiole" type (D) often grades into the large, erect type (A). B and C represent offshoots or ramets. Abbreviations are as follows: (ar) adventitious roots; (bb) bud bract; (in) inflorescence; (is) leaf isthmus, a constricted area between the petiole (pt) and lamina (la); (pd) peduncle; (pl) primary leaf; (rh) rhizome or stem; (sp) spathe; (st) stolon
low specific gravity of the bulbous petioles tends to keep the shoot erect. (Penfound and Earle, 1948). As the mat becomes further developed and the leaves elongate, the extensive interweaving of the plants tends to hold the shoots erect and the petioles cease to function as "floats" (Fig. 2). The adventitious root system is usually suspended in the water although the plants may become rooted if stranded in moist soil or in shallow water. The roots tend to be "bottlebrush" in form with a central axis and numerous unbranched side roots. Weber (1950) examined the roots on one average size plant and found the total linear length of the 158 adventitious roots and all lateral roots to be 11,481 m with a total area of 7.31 m². Some data suggest that the relative extent of development of the root system may be inversely related to the availability of dissolved nutrients (Knippling et al. 1970).

The Natural Enemies of Waterhyacinth

The Waterhyacinth Weevils

*Neochetina eichhorniae* Warner and *N. bruchi* (Hustache)

**Coleoptera: Curculionidae**

Weevils in the genus *Neochetina* are classified into the subfamily Erirhiniae and the tribe Bagoini. *Neochetina* is comprised of six species whose native range is primarily South and Central America (O'brien, 1976). All are semiaquatic, are covered with a layer of very dense, water-repellent scales, and feed on species of plants in the family Pontederiaceae.

The adults of *N. bruchi* and *N. eichhorniae* can usually be distinguished by the color and pattern of the scales covering the elytra (O'brien, 1976; DeLoach, 1975, Warner, 1970). *N. bruchi* ranges in color from uniform tan or brown with no distinct markings to brown with a broad, crescent-shaped or chevron-like tan band across the elytra. *N. eichhorniae* never has the tan band and is usually
Figure 2. A stylized representation of a waterhyacinth mat showing how smaller plants at the fringe and nearest the open water surface grade into the larger shoots nearest the shore where intra-shoot competition is intense.
gray mottled with brown. The color pattern is associated with the scales and specimens may be difficult to identify if the scales are missing or the specimens are dirty or wet. Both species have two short, shiny, dark lines on the elytra on either side of the mid-line. This short line is actually a tubercle or ridge and its position varies between the two species. On *N. bruchi* the tubercles are situated very near mid-length. Although the position of the tubercles is more variable on *N. eichhorniae*, they are usually situated further forward, in front of mid-length. A more subtle character separating these two species concerns the lines (striae) which run lengthwise and nearly parallel to one another on the elytra. These striae are actually shallow grooves. On *N. bruchi* the striae are relatively fine whereas on *N. eichhorniae* they are relatively coarse. This gives *N. bruchi* an overall smoother textural appearance than *N. eichhorniae*. For further information on the identification of these two species, the reader should consult Warner (1970), DeLoach (1975), or O'brien (1976).

The eggs, larvae, and pupae of both species are very similar and virtually indistinguishable from one another. Identification of the immature stages is difficult.

Eggs are whitish, ovoid, and about 0.75 mm in length. Since they are embedded in the plant tissue, they can usually only be found by dissecting the plant under a microscope.

Larvae are white or cream-colored, with a yellow-orange head. They have no legs or prolegs, only enlarged swellings with setae (small hairs) where the legs should be. The posterior end of the abdomen is blunt and a pair of spiracles (breathing tubes) project upward, somewhat spur-like, on the last abdominal segment. These spur-like spiracles presumably allow the larva to obtain oxygen by inserting them into the plant tissue. When the larvae first emerge from the
egg they are very small (ca. 2 mm in length) and cylindrical in shape. The fully grown third instar larva is somewhat grub-like, C-shaped, and ca. 8-9 mm in length.

Pupae are white and resemble the adults. The pupa is enclosed in a cocoon formed among the lateral rootlets and attached to the main root axis below the water surface. These appear as small balls or nodules ca. 5 mm in diameter on the roots usually near the rhizome.

Eggs of both species of *Neochetina* are deposited directly in the plant tissue. The female chews a hole into the lamina or petiole in which to lay eggs. *N. eichhorniae* deposits only one egg in each hole whereas *N. bruchi* deposits several. Either species may also place the eggs around the edge of leaf abrasions created by the feeding of the adults. DeLoach and Cordo (1976a) reported that *N. bruchi* preferred to oviposit in leaves with inflated petioles and especially those at the periphery of the plant while *N. eichhorniae* preferred the tender central leaves or the ensheathing stipules at the leaf bases. We have found that eggs of *N. eichhorniae* are rare in the youngest leaves and are usually found in those of intermediate age. Eggs are most prevalent in the basal portion of the petioles where the stipules are somewhat open and a space is available for the adults to congregate.

The eggs hatch within 7-10 days at 75°F.* The first instar larvae which are very small (head diameter of ca. 0.3 mm) burrow under the epidermis and work their way toward the base of the leaf. They pass through a total of three larval instars. The first molt occurs when the larvae are about 10 days old and the second about 2 weeks later. As they grow larger, the galleries or feeding burrows become larger. Third instars are generally located at the petiole bases.

* A table of factors for converting U. S. customary units of measurement to metric (SI) units is presented on page xv.
and may enter the stem (rhizome) and excavate small pockets at the point of insertion of the leaf. They occasionally burrow up the stem to enter the base of younger petioles and sometimes reach the stem apex and destroy the apical bud. The larval period probably requires 30-45 days with *N. bruchi* developing somewhat faster than *N. eichhorniae*.

The fully developed larvae burrow out of the stem and move to the upper root zone just under the surface of the water. They cut off the small lateral rootlets and form a spherical parchment-like cocoon around themselves. This cocoon is attached to one of the roots. Curiously, at the point of attachment, the larva chews a notch into the root. This notch supposedly functions in gas exchange between the hollow inside of the cocoon and the vascular tissue of the plant. After the cocoon is formed the larva molts a third time and becomes a pupa. This is the inactive stage when the transition from larva to adult occurs. It is not known with certainty how long this stage lasts, but best estimates indicate about 30 days.

As the adults emerge from the cocoon they appear to split the cocoon, push the opening wider with their legs and pull themselves out through the split. Once they are out, they climb up onto the emergent leaves of the plant to feed and mate. The females weevils begin to lay eggs within a few days after emerging from the pupa and most are deposited within the first week. A single female *N. bruchi* will deposit up to 300 eggs but *N. eichhorniae* deposits only about 60. DeLoach noted that about 90% of the eggs are deposited within a month after the female emerges although the adults may live over 9 months. For further details on the biology of these species, see the articles by DeLoach and Cordo (1976a,b).
The Waterhyacinth Moth

*Sameodes albiguttalis* (Warren)

Lepidoptera: Pyralidae

The eggs of *Sameodes albiguttalis* are small (ca. 0.3 mm), spherical, and creamy-white. The shape of the egg is often irregular because the chorion (egg shell) is soft and the adult female often pushes them into cracks and crevasses in the plant thus distorting their shape. As the embryo develops the egg becomes progressively darker. Just prior to hatching it appears black due to the visibility of the black head of the larva within the egg. Complete development of the embryo usually requires 3-4 days at 25°C.

The newly emerged larva measures ca. 1.5 mm in length, is brownish with darker spots, and its head is black to dark brown. As the larva grows it sheds its skin and passes through 5 instars. The fully grown 5th instar larva is ca. 2 cm long, has a dark orange head and a cream-colored body, and is covered with conspicuous dark brown spots. Completion of the 5 larval stages requires ca. 2 weeks.

When the larva is fully grown it seeks out a fairly large, relatively intact waterhyacinth leaf petiole and burrows into it. It excavates an elliptically shaped cavity in the middle of the petiole with a tunnel extending from one end. This tunnel leads from the cavity to just beneath the outside surface of the petiole and the end remains covered by the leaf epidermis. The larva then forms a cocoon by spinning silk around itself and creates a lining within the cavity which extends up the entire length of the tunnel. Soon afterwards it sheds its last instar larval skin and becomes a pupa. It is inactive during this stage (which lasts 7-10 days) while many complex internal changes take place which alter its structure to that of an adult moth. After it is fully
formed it breaks out through the head end of the pupal skin, crawls through the silk-lined tunnel, and breaks through the thin layer of epidermis at the end to exit from the petiole. The exit tunnel is necessary since the adults no longer have chewing mouth parts and could not otherwise escape from within the petiole.

The adult moths are frequently found resting on the underside of waterhyacinth leaves. The females are generally darker in color than the males but color is extremely variable in both sexes. The forewings range in color from brown to golden with the hindwings more consistently golden. There is usually a distinct white spot at mid-length towards the leading edge of the forewing and a dark spot in the center of the hindwing. The hind edges of the segments of the body are almost always white giving the appearance of white rings around the abdomen. The adults probably live no more than a week to 10 days and many fall prey to dragonflies, spiders, lizards, frogs, and other predators.

Mating occurs shortly after emergence from the pupa and the female lays the majority of her eggs the following night. A female will deposit ca. 450 eggs but up to 600 is not unusual. The entire life cycle from egg to egg requires 3-4 weeks.

A few other species of lepidopteran larvae feed on waterhyacinth but the only one likely to be confused with S. albicuttatus is Samea multiplicable Guenée. The larvae of this species also have the conspicuous brown spots but these are generally not as dark as on S. albicuttatus. Curiously, when S. multiplicable feeds on other host plants, such as Pistia stratiotes L. (as they are likely to do), the spots are not at all conspicuous. A fully grown S. multiplicable larvae is smaller (ca. 13 mm) than S. albicuttatus (ca. 18 mm) and has a pale brownish head instead of a dark brown or orange one. The pupae and mode
of pupation are also similar in these two species, as are the adults. See Center et al. (1982) for characteristics useful in separating these two species.

The Pickerelweed Borer

**Arzama densa** Walker

**Lepidoptera:** Noctuidae

*Arzama densa* is a species of moth indigenous to the United States and should probably be included in the genus *Bellura* along with the *Nuphar* borer (*B. gortynoides*) and the cattail borer (*B. obliqua*). The native host of *A. densa* is pickerelweed (*Pontederia cordata* and *P. lanceolata*) but, at times, when pickerelweed is scarce or the moth populations are high, the insects may switch to waterhyacinth. Extensive damage to waterhyacinth is rare because of the large complex of diseases and parasitoids which severely reduce *A. densa* population (Vogel and Oliver, 1969; Center, 1976).

The adult female deposits a mass of approximately 40 eggs on the abaxial surface of a waterhyacinth or pickerelweed lamina. The egg mass is covered with cream-colored hair-like scales from a tuft on the tip of the female's abdomen which adheres by way of a mucous-like secretion. The egg mass is about 10 mm in diameter, and plano-convex. Each egg is ca. 1 mm in width and length and a single female produces up to 300 eggs. This clustering mode of oviposition seems to protect a portion of the eggs from a scelionid parasitoid (*Telenomus arzamae* Riley).

The eggs hatch in ca. 6 days and the first instar larvae are ca. 2 mm long, have a conspicuous black ca. 0.5 mm diameter head, with a black prothoracic shield and light brown to somewhat pinkish body. Second and third instars have yellowish-brown, ca. 0.7 mm and 1.0 mm diameter heads, respectively, grayish prothoracic shields, with amber-colored dorsal body surfaces and whitish ventral
surfaces and, by the end of the third instar, attain a length of ca. 2.0 cm. Fourth instars have yellowish, ca. 2.3 mm diameter heads, brown cervical shields, yellowish-brown dorsums and white ventrums, and attain lengths of ca. 3.0 cm. The color gradually darkens through to the seventh instar larvae which have dark reddish-brown, ca. 3.3 mm diameter heads, brown prothoracic shields, very dark brown to charcoal gray dorsums, pale cream-colored ventrums, and attained lengths of 6.0 cm.

Pupation occurs within a burrow in a leaf petiole following a 3 day prepupal period and the pupa is not enclosed in a cocoon. The pupa is large (ca. 3.0 cm) and dark reddish-brown in color and pupation requires about 10 days. The adults are brown to reddish-brown, rather stout, and somewhat fuzzy in appearance. Complete development from egg to egg requires ca. 50 days.

The damage to waterhyacinth created by *A. densa* is similar to that caused by *S. albiguttalis* but more severe. Early instar larvae scrape the leaf epidermis causing extensive abrasions. Later instars burrow extensively within the petioles, and the larger larvae may create deep burrows within the rhizome and kill the shoot. *A. densa* damage is readily distinguished from that of *S. albiguttalis* by the larger galleries and the coarser texture of the frass.

**The Waterhyacinth Mite**

*Orthogalumna terebrantis* Wallwork

*Acarina: Oribatei: Galumnidae*

Adult waterhyacinth mites are shiny-black, ca. 0.3 mm wide by ca. 0.5 mm long, tear-drop shaped, and narrowed anteriorly. Females cut a small round hole in the adaxial surface of a waterhyacinth lamina in which to oviposit and oviposition occurs primarily on very young leaves. Eggs hatch in 7-8 days (at 25°C) and produce small (less than 0.24 mm), whitish, slow-moving larvae which bear 3
pairs of legs. Nymphs bear four pairs of legs and are amber colored and the three nympha\nal stages (proto-, deuto-, and tritonymphs) are distinguishable primarily on the basis of size (maximum lengths 0.32 mm, 0.39 mm, and 0.50 mm, respectively). Total development through larval and nympha\nal stages requires ca. 15 days (at 25° C).

Feeding damage by the mites is restricted to the laminae. The larvae produce small reddish spots on the abaxial leaf surface and the nymphs produce galleries that extend distally towards the leaf apex. These galleries are located between the parallel leaf veins and attain maximum lengths of 6 mm. The adults emerge from the galleries through small, round exit holes at the distal end of the gallery. When populations are high, large numbers of galleries (up to 2500 per lamina) may be present. These high numbers cause desiccation of the leaf and result in the lamina turning brown. Severe damage, however, is usually confined to a small area or a few plants. Rarely is damage extensive enough to effectively control waterhyacinth populations.

The above discussion is derived from information in the paper by Cordo and DeLoach (1976).

Spider Mites

* Tetranychus urticae*

Acarina:Protostigmata:Tetranychidae

Spider mites are rather large mites with plump bodies many of which cause serious damage to economically important crops. They form colonies in "webs" which frequently envelop the foliage. Eggs are small, spherical, and yellowish and normally hatch in 3-5 days. Development progresses through four instars including the larva, protonymph, deutonymph, and adult. Males develop from unfertilized eggs while females develop from fertilized eggs.
The mites feed upon the plant juices by piercing the epidermis of the leaf with two sharp, slender, lance-shaped structures attached to the mouth. The damage is first noticeable as small, diffuse, discolored patches composed of very small, scratch-like marks on the leaves. The mite populations increase rapidly and may ultimately cause the wilting and complete desiccation of the leaves. In severe cases the plants appear burnt. Damage is normally very sporadic and patchy, however, and waterhyacinth seems to quickly recover from it.

The species of spider mite most commonly found on waterhyacinth is *T. urticae* (Koch). *T. urticae* is characterized by two color phases, a carmine phase and a green-yellow phase. Gordon and Coulson (1969) also listed *T. tumidus* Banks and *T. gloveri* Banks as occurring on waterhyacinth.

**Pathogens**

Conway et al. (1974) listed 27 fungal genera associated with waterhyacinth but confirmed as pathogenic only three species. These three species were *Acremonium zonatum* (Sawada) Gams, *Bipolaris stenospila*, and *Cercospora piaropi* Tharp (incl. *C. rodmanii* Conway). This list of fungi was later expanded (e.g. Charudattan et al., 1978) but it is uncertain just how many pathogenic species are now known although there are at least eight (Gopal and Sharma, 1981). For purposes of this study, pathogens were diagnosed as *Acremonium zonatum*, *Cercospora* sp., or included within miscellaneous factors.

**Acremonium zonatum**

Symptoms of this fungal leaf spot consist of oval to irregularly shaped lesions which gradually enlarge and coalesce. The spots become distinctly zonate and are light brown with alternating, thin, dark brown bands which are more or less concentric. The growth of colonies is slow and is favored by high
humidity and moderate temperatures (20-30°C). Rintz (1973) notes that A. zonatum does not seem capable of killing or seriously hindering the growth of waterhyacinth.

For more information on this species consult the papers by Rintz (1973), Martyn and Freeman (1978), and Freeman et al. (1974).

Cercospora spp.

In 1972, a leaf spot disease, subsequently identified as Cercospora piaropi Tharp, was found on waterhyacinth in Florida (Freeman and Charudattan, 1974). In 1973, Conway (1976a) identified a Cercospora which he thought was sufficiently different to be considered a new species. This species was isolated from waterhyacinth in Rodman Reservoir and named C. rodmanii Conway. Separation of these two species is best left to the pathologists and, in this study, no attempt has been made to distinguish between them.

Symptoms of Cercospora spp. are evident as small, oval, 1.5 to 4.0 mm spots on waterhyacinth lamina. The smaller spots are purplish-black but as they increase in size they develop a tan-colored center. The lesions often coalesce around the leaf edges on the distal portion of the lamina which results in a general necrotic condition. Large spots may be faintly zonate.

Under natural conditions, Cercospora spp. does not seem to be sufficiently virulent to adversely affect waterhyacinth.

For more information see the papers by Freeman and Charudattan (1974), Conway and Freeman (1977), and Conway (1976 a,b).

Miscellaneous Factors

Throughout the period of this study a plethora of factors were observed to result in the death of leaves and many of these were difficult to identify. Pathogens, in particular, are nearly impossible to distinguish in the field.
unless very distinct symptoms are displayed. For this reason, any leaf mottling or spotting, any tip die-back or general necrotic condition including normal senescence, or any other symptom that could not be ascribed as being due to a specific cause was placed in a miscellaneous category.

**Browsers**

Several non-specific herbivores including vertebrates such as the American Coot (*Fulica americana*), Pond Sliders (*Pseudemys scripta*), and other birds, turtles, and even cattle will casually browse on waterhyacinth leaves. This results in the removal of a portion of the leaf but it is not always easy to determine which critter has done the damage. In these cases, the damage was placed in a category which indicated that a portion of the leaf was missing. Also included in this category was wind or wave injury or any other factor which resulted in leaf breakage or partial loss.

**OBJECTIVES**

The objectives of this study were as follows:

1) Determine the relative importance of various biological control agents as contributing factors to the decline of waterhyacinth leaves as related to the age structure of the leaf population.
2) Determine the rate of replacement in the leaf population by measuring leaf production on tagged plants.
3) Determine the rate of mortality of leaves in the leaf population by estimating the age at which leaves die on tagged plants.
4) Evaluate *S. albicrteralis* in terms of the percentage of shoots affected in the population and its relative importance as a factor in leaf mortality, turnover, and production.
5) Compare various sites in terms of the rate of growth of the waterhyacinth mat as affected by biological factors.
METHODS AND MATERIALS

Because of the diversity of methods and procedures employed over the term of this study, a cross-indexed site by procedure table is provided (Table 1). Each procedure is described separately below. The location of each site is shown in Fig. 3.

Procedure 1

A 100 X 100 cm frame made of 3/4 inch PVC pipe was superimposed upon the waterhyacinth mat to define the boundaries of a sample area. All plants within the frame were removed, placed into plastic bags, and transported to the laboratory for detailed examination. Ten plants were randomly selected from each bag and the following measurements and observations were made on each:

1.) Length of the third leaf (as counted outwards from the center of the rosette).
2.) Root length - measured from the base of the leaf rosette to the tip of the longest root.
3.) Total number of living leaves (leaves more than 50% green).
4.) Total number of dead leaves (less than 50% green).
5.) Sameodes albiguttalis - Number of eggs, larvae, pupae, and leaves damaged.
6.) Arzama densa - Number of larvae, pupae, and leaves damaged.
7.) Neochetina spp. - Number of adults, larvae, pupae, and leaves damaged.

Procedure 2

Three sites were selected in Everglades conservation area 3A, two of which were in Broward Co. with the third in Dade Co. Access to the sites necessitated the use of an airboat. Samples within the waterhyacinth mat were obtained by
Figure 3. The location of the 15 sites in Florida at which studies on the efficacy of S. albipalpis were conducted between 1978 and 1982.
Table 1. A list of study sites with Universal Transverse Mercator (UTM) coordinates, the dates and procedures employed, and the general location of each site.

<table>
<thead>
<tr>
<th>SITE</th>
<th>LOCATION</th>
<th>UTM COORDINATE</th>
<th>OBSERVATION DATES</th>
<th>PROCEDURE USED</th>
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<tr>
<td>7</td>
<td>Everglades Conservation Area 2A, Sawgrass Recreation, Broward Co.</td>
<td>NV5401</td>
<td>Oct 80 - Nov 80</td>
<td>5</td>
</tr>
<tr>
<td>8</td>
<td>Snake Creek, 6 mi. E Sanford, Volusia Co.</td>
<td>MB8386</td>
<td>Oct 80 - Dec 80</td>
<td>5</td>
</tr>
<tr>
<td>9</td>
<td>Lake Okeechobee</td>
<td>MV9481</td>
<td>Nov 80 - Feb 81</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>a. Fisheating Bay, Glades Co.</td>
<td>MV1798</td>
<td>Apr 81 - Jul 81</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>b. King's Bar Island, Okeechobee Co.</td>
<td></td>
<td>Jan 82 - Jul 82</td>
<td>8,9,10</td>
</tr>
<tr>
<td>10</td>
<td>St. Johns River, 3 mi. W Deland, Lake Co.</td>
<td>MC6407</td>
<td>Jan 81 - Sep 81</td>
<td>6</td>
</tr>
<tr>
<td>11</td>
<td>Coral Springs Waste Water Treatment Plant, Broward Co.</td>
<td>NV7606</td>
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<td></td>
<td>a. Asphalt ponds</td>
<td></td>
<td>May 81 - Sep 81</td>
<td>6</td>
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<td></td>
<td>b. Earthen ponds</td>
<td></td>
<td>Oct 81 - Nov 81</td>
<td>7,8,9</td>
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<tr>
<td>12</td>
<td>Lake Trafford, 3 mi. W Immokalee, Collier Co.</td>
<td>MV5222</td>
<td>Aug 81 - Sep 81</td>
<td>6</td>
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<tr>
<td>13</td>
<td>Wekiva River, 6 mi. NE Apopka, Orange and Seminole Counties</td>
<td>MB7858</td>
<td>Oct 81 - Nov 81</td>
<td>7,8,9</td>
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<tr>
<td>14</td>
<td>Canal M, 2.5 mi. W West Palm Beach, Palm Beach Co.</td>
<td>NV8559</td>
<td>Dec 81 - May 82</td>
<td>7,8,9</td>
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<td>Jun 82 - Oct 82</td>
<td>8,9,10</td>
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<tr>
<td>15</td>
<td>Cypress Creek Canal, Pompano Beach at Palm-Aire, Broward Co.</td>
<td>NV8201</td>
<td>Jan 82 - Jun 82</td>
<td>7,8,9</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Jul 82 - Aug 82</td>
<td>8,9,10</td>
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</table>
placing a 0.25 m² frame (50 X 50 cm) made of 1.5 inch diameter PVC pipe over the plants.

All of the waterhyacinth shoots were removed from the sample frame, placed in plastic bags, and transported to the laboratory. There the total number of waterhyacinth shoots in each sample was counted and the petioles were dissected and examined for the presence of *S. albiguttalis* pupae and larvae. The entire sample was dried at 70°C and then weighed.

The following data were derived:

1) a) Number and percentage of waterhyacinth shoots damaged by *S. albiguttalis*.
   b) Percentage of the total number of shoots with *S. albiguttalis* damage to the apical bud.

2) Number of *S. albiguttalis* larvae per shoot.

3) Number of *S. albiguttalis* pupae per shoot.

4) Standing crop (dry weight).

Procedure 3

Transects were established within the waterhyacinth mat with sampling points at 10 meter intervals. At these sites, the waterhyacinth mat was extensive and covered most of the water surface requiring watershoes for access to the sites. Ten plants were removed from the mat and examined at each sampling point.

The following data was collected from each plant:

1) Root length.

2) Total number of living leaves.

3) Length of third youngest leaf.

4) Length and position of the longest leaf.
5) Number of adult *Neochetina* spp. per plant.

6) Number of *Neochetina* spp. larvae per plant.

7) Number of *Sameodes albicuttalis* larvae per plant.

8) Number of *S. albicuttalis* pupae per plant.

9) Number of *Arzama densa* larvae per plant.

10) Number of *A. densa* pupae per plant.

11) Leaf condition of each leaf on each plant, rated 1 through 4 based upon the percentage of the leaf remaining alive, as follows:
   a) 1=Alive - Over 90% green.
   b) 2=More alive than dead. - Greater than 50% green.
   c) 3=More dead than alive. - Less than 50% green.
   d) 4=Dead - No green.

12.) Injury caused by various agents to each leaf rated as 1 (present) or 0 (absent), as follows:
   a) *Sameodes albicuttalis* larval damage
   b) *Neochetina* spp.
      (1) Adult feeding.
      (2) Larval damage.
   c) *Arzama densa* larval damage.
   d) Red spider mite (*Tetranychus* spp.) damage.
   e) Waterhyacinth mite (*Orthogalumna terebrantis*) damage.
   f) Fungus (Pathogens)
      (1) *Cercospora* sp.
      (2) *Acremonium zonatum*
   g) Miscellaneous factors
Procedure 4

This procedure was implemented in order to estimate the impact of *S. albiguttalis* infestation upon a waterhyacinth fringe developing along a canal bank. The waterhyacinth mat was periodically mapped using a transit and stadia pole. Two transit stations were established along one bank of the canal and each station was marked with a 1" x 2" pressure treated stake placed 2 feet into the ground with only the top 2 inches protruding. The distances and compass bearings of points at the edge of the waterhyacinth mat were measured, the coordinates thus obtained were transferred to graph paper to produce the map, and the area of waterhyacinth coverage was then measured on the map with a compensating polar planimeter. Growth over time was evaluated on the basis of changes in coverage.

In addition to the mat measurements, 20 randomly selected plants were examined at each of 10 points located at 10 m intervals along the mat fringe to estimate *S. albiguttalis* population intensity. Counts of the following types of *S. albiguttalis* damage were obtained:

1) **Type A** - number of plants with "windows" in petioles. "Windows" consist of areas in the leaf petiole where larvae have fed immediately below the epidermis creating a concavity covered by the hyaline epidermis.

2) **Type B** - Number of plants with extensive damage to the youngest leaves and the apical bud destroyed.

3) **Both** - Number of plants with both Type A and Type B damage.

From this information the percentage of plants damaged and severity of the insect infestation was determined.

Aerial photographs (color and infrared) were taken in order to record
extent and general condition of the waterhyacinth mat.

Procedure 5

Observations on the same plants over extended periods of time have been found to be the best way to evaluate the effectiveness of a biological control agent. This procedure was our first attempt to tag plants and thus be able to identify them on subsequent dates.

In August 1980 at site 6, 20 shoots with no apparent *S. albicuuttalis* damage were selected for tagging. The shoots were selected along a transect at equal intervals 2.5 meters apart. A plastic nursery label was placed at the base of the lamina of the first four leaf positions (the 4 youngest leaves) of each shoot. Each was given a number and that number and the date were marked on the tags. Data were recorded for all leaves of each shoot. The position of each leaf was determined, each was evaluated as to its condition, and all factors causing damage to it were noted. Condition was rated from 0-10 according to the proportion of the entire leaf that was green (undamaged). If it was entirely dead, the rating was 0. If it was entirely alive (relatively no damage), the rating was 10.

The following factors were rated on each leaf as present or absent (1 or 0):

1) *S. albicuuttalis* larval damage
2) *Neochetina* spp. larval damage
3) *Neochetina* spp. adult damage
4) *Arzama densa* larval damage
5) *Orthogalumna terebrantis* (waterhyacinth mite) damage
6) *Tetranychus urticae* (spider mite) damage
7) *Acremonium zonatum* leaf spots
8) Miscellaneous damage (includes pathogens, senescence, etc.)

9) Partial leaf - a portion of the leaf missing

The length of the third leaf of each shoot was determined by measuring the distance from the insertion of the petiole base to the apex of the lamina.

Plant density was recorded in the vicinity of alternate tagged shoots. A PVC pipe frame with an inside area of 0.25 m² (50 X 50 cm) was randomly placed on the waterhyacinth mat. The number of shoots within the frame were counted. A shoot was considered within the frame only if its youngest leaf was in. A 1 m tall PVC pole, which was filled with foam and weighted with lead shot at one end, was placed near each tagged shoot to mark the location.

By October 1980, it became evident that each factor affecting leaf mortality should be rated according to severity. From this date on the procedure was modified at sites 6 and 7, whereby the leaf condition was rated from 0-10 as previously described but the factors which affected leaf condition were rated on a 0-4 scale as follows:

0 = no damage
1 = 1-25% of the leaf damaged
2 = 26-50% of the leaf damaged
3 = 51-75% of the leaf damaged
4 = 76-100% of the leaf damaged

This rating method enabled the determination of the causal factors of leaf and plant mortality.

Procedure 6

By November 1980, it was determined that the 0-4 rating scale was also inadequate and an even more sophisticated rating method was employed. Ten shoots, each with no symptoms of S. albi-guttalis damage, were selected at each
The four to six youngest leaves on each shoot were tagged by placing a plastic nursery label around the base (isthmus) of the lamina of each leaf. Each tag was labeled so as to identify each individual shoot and each leaf for reference at a later date. Data were recorded only for the first four to six leaves at the first observation depending on the age and size of plants because the oldest leaves were usually dead and sloughed off before the next observation date.

The oldest tagged leaf was initially designated as leaf number 01 so that as new leaves were produced, successive numbers were used. Therefore, at the first tagging, position four was labeled leaf number 01 and position one was labeled leaf number 04. As new leaves were produced during the interval between sampling periods, they were given successive leaf numbers and the number of new leaves produced was determined. By the second observation all positions were tagged.

After the leaves were tagged, the position of each leaf was identified and the condition of each leaf was evaluated. Symptoms of damage to the leaf caused by various mortality factors were diagnosed and rated according to the percentage of the leaf affected:

1) Condition: The proportion of the leaf possibly remaining functional, rated from 0-100 according to the relative amount of green tissue remaining or not affected by a damaging agent. If entirely dead, rating = 0, if entirely alive (no damage), rating = 100. The lamina and the petiole were each considered to represent 50% of the total leaf.

2) Adult Neochetina spp. feeding: rated from 0-100 according to the proportion of the leaf surface removed by adult feeding, i.e., that proportion covered with feeding lesions.
3) Larval Neochetina spp. feeding: rated from 0-100 according to the percentage of the leaf affected by larval feeding. If the entire base of the petiole was damaged by larval feeding, the leaf was considered non-functional and a damage value of 100% was assigned and leaf condition was considered to be 0%.

4) Sameodes albiguttalis larval feeding: rated from 0-100 as with Neochetina larval feeding. If a petiole was girdled by Sameodes, the proportion above that point was no longer functional and rated accordingly. If Sameodes had tunneled the growing bud, the youngest leaf was assigned a damage value of 100%.

5) Arzama densa larval feeding: rated from 0-100 as with Neochetina and Sameodes larval feeding.

6) Spider mite (Tetranychus urticae) damage: rated according to the proportion of the leaf damaged. The damage was normally found only on the lamina resulting in a maximum possible rating of 50%.

7) Waterhyacinth mite (Orthogalumna terebrantis) damage: rated same as spider mite damage.

8) Acremonium zonatum: rated from 0-100 according to the proportion of the leaf surface covered with zonal leaf spots.

9) Cercospora: rated from 0-100 according to the proportion of the leaf surface covered.

10) Miscellaneous: possibly any one of a number of factors which cause the leaf to take on a mottled pattern including naturally occurring symptoms of senescence. The exact causes of these symptoms were often unknown. These were rated from 0-100 according to the proportion of the leaf obscured by this mottling.
11) Frost damage: rated from 0-100 according to the percentage of the leaf damaged by freezing temperatures.

12) Partial leaf: rated from 0-100 according to the portion of the leaf missing. This could result from feeding by armyworms or grasshoppers, mechanical breakage, browsing by coots or turtles, or any factor causing a portion of the leaf to be missing.

13) Desiccation: damage to the leaves caused by drought or stranding. This was rated from 0-100 according to the proportion of the leaf that had turned brown or yellow.

Plant density was counted in the vicinity of each tagged shoot by randomly placing a 0.25 m² PVC pipe frame on the mat and counting the number of shoots thus enclosed.

The length of the third position (third youngest) leaf was recorded for each shoot at each observation by measuring the distance from the insertion of the petiole base to the apex of the lamina.

At sites where it was possible for the tagged plants to float away, it was necessary to anchor them in place. A 0.25 m² square frame made of PVC pipe was carefully placed around the tagged plants so as not to disturb their spacing and the frame was tied to a stake. The number of plants initially inside the square was equivalent to the natural plant density, but as growth within the enclosed area caused plant density to become greater than that of the surrounding area, it became necessary to periodically thin them. Plant density both before and after thinning the plants was recorded.

Procedure 7

This procedure was used at field sites where the waterhyacinth population did not cover the entire water surface, the population was actively growing, and
plants with the swollen, inflated type of leaf petioles were abundant at the periphery of the mat. Shoots (30-100) with inflated leaf petioles were selected at random from the edge of the mat (except at site 4 where the shoots were selected from within an established population which had no growing fringe). The four youngest leaves of each shoot were tagged with a plastic tag below the lamina on the smallest part of the petiole. Each shoot was assigned a number, the number and the tagging date were placed on each tag, the plants were observed on successive dates, and the number of new leaves produced and the length of the third youngest leaf were recorded each time. Data were collected on each leaf of each shoot. The following factors were examined and rated on a 0-100% rating scale:

1.) **Condition** = Percentage of the leaf remaining green, i.e. that proportion of the entire leaf not affected by a damaging factor (mortality factor).

2.) **Sameodes albiguttalis damage** = Percentage of leaf destroyed by *S. albiguttalis* larvae. Ten plants from each of 10 replicates were tagged and examined.

**Procedure**

A 0.25 m² frame (50 x 50 cm), constructed of 1.5” diam. PVC pipe, was randomly placed in ten locations within the waterhyacinth mat to delineate sampling areas. The total number of waterhyacinths shoots on which the youngest leaf was within the sample area was recorded in each sample. *Sameodes* damage, when found, was classified according to five types of damage. The following list describes the types of damage recorded.

<table>
<thead>
<tr>
<th>Classification</th>
<th>Description</th>
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<tr>
<td>Minor</td>
<td>Areas where usually early instar larvae had fed within the petiole in such a way as to create a concavity just under the</td>
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epidermis but leaving the epidermis intact. The translucent epidermis covering the cavity gives the impression of a "window" in the side of the petiole.

**Significant** A *S. albiguttalis* larva, usually late instar, had tunneled the petiole of the youngest leaf and severely damaged it. The apical bud at the tip of the rhizome not damaged, however.

**Critical** Combination of classifications 1 and 2. The shoot was extensively damaged but still able to produce leaves.

**Lethal** The apical bud located at the base of the youngest leaf at the apex of the rhizome had been destroyed. This type of damage stops the shoot from producing new leaves and the shoot ultimately dies.

** Fatal** The apical bud had been destroyed, leaf production halted, and existing leaves had extensive damage.

From this sampling procedure we collected the following data:

1.) Total number of shoots per unit area.
2.) Number of shoots with no *Sameodes* damage.
3.) Proportion of shoots with damage caused by *S. albiguttalis* larvae and the frequency of each type of damage.
4.) Total number of dead shoots per unit area.

As the plants from each sample were examined, 4 shoots (40 total) were selected at random for detailed observations (see procedure 9).

**Procedure 9**

Four shoots were randomly collected from each of ten 0.25 m$^2$ samples (40 shoots total) at the field sites and placed in plastic bags. These were then transported to the laboratory for further examination.
In the laboratory, the stem position of each leaf was determined and the condition of each leaf was evaluated. Factors causing deterioration of the leaves were diagnosed and rated on a scale of 0-100% based upon the percentage of the leaf affected. These factors are listed below:

1.) **Condition:** % of leaf unaffected by a mortality (damaging) factor.
2.) **Adult *Neochetina* spp. feeding:** percentage of leaf surface destroyed by feeding.
3.) **Neochetina** spp. larval feeding: percentage of the leaf showing serious injury due to larval burrowing.
4.) **Sameodes albiguttalis** larval feeding: same as number 3.
5.) **Arzama densa** larval feeding: same as number 3.
6.) **Red mite (**Tetranychus urticae**) damage:** percentage of leaf surface area affected.
7.) **Waterhyacinth mite (**Orthogalumna terebrantis**) damage:** percentage of leaf area affected.
8.) **Acremonium zonatum:** percentage of leaf surface area covered with zonate spots.
9.) **Cercospora:** percentage of leaf surface showing symptoms of infection.
10.) **Miscellaneous:** percentage of leaf browned or yellowed, usually due to unknown factors which cause browning of the leaves or a mottled pattern on the laminae.
11.) **Frost damage:** percentage of leaf damaged.
12.) **Partial leaf:** percentage of leaf area missing.
13.) **Senescense:** percentage of leaf yellowed due to aging process.

The following measurements were recorded for the third youngest leaf of each of the 40 shoots:

1.) **Leaf length,** distance from petiole base to lamina tip.
2.) Root length, maximum length of roots.
3.) Lamina length, base of lamina to apex.
4.) Lamina width, at widest point.
5.) Petiole length, from petiole base to base of lamina.
6.) Petiole diameter, at mid-point or widest point.
7.) Petiole diameter, at base.

Procedure 10

Waterhyacinth leaf production was determined by tagging (30 to 100) shoots. The tag was placed around the youngest leaf petiole. On a subsequent date these tagged plants were re-examined. The youngest leaf of each plant was re-tagged and the number of leaves produced between observations was counted. New plants were tagged to replace tagged plants that had died or could not be found.
SITE DESCRIPTIONS

The following pages contain a list and description of each study site. Figure 3 shows the general location of each site in the state.

Site 1: Sawgrass Lake, Pinellas County

UTM Reference: LA3586

Site 1 was the second of the original 20 *S. albicultalis* release sites and was located in a canal flowing into Sawgrass Lake. Sawgrass Lake, located in Pinellas County near Pinellas Park north of St. Petersburg, is in a park administered by the county school system as a nature conservation area. The study area was in the canal which flows into Sawgrass Lake at its northeast end. Data were collected near the road culvert at Rt. 600. The main water supply to the canal is drainage from surface runoff of the surrounding urban areas and limited agricultural land to the north. Water flow was from the northwest into the canal and into Sawgrass Lake, southeast through the lake and out through a canal at the southeast end, then east to Tampa Bay (Fig. 4). The water level and canal flow varied considerably with seasonal rainfall.

The canal periodically flooded and the waterhyacinth population thereby "washed out." Regrowth occurred along the canal banks as a fringe of small shoots at which time these shoots bore the inflated type of petioles. The plants usually filled in eventually and completely covered the water surface in the canal.

Sampling points were designated at 10 meter intervals along the canal and pressure treated 1" X 2" stakes were used to mark each point on the canal bank. Water shoes were used to collect plant samples. Samples were collected according to the methods described in Procedure 1. The site was photographed from the culvert towards the east in a view down the canal as well as at each...
Figure 4. A map showing the location of site 1 in a canal which discharged into Sawgrass Lake in Pinellas County
sample location. Aerial photographs were taken when a significant change in the site was noted.

Site 2: Leon's Orchid Isles
UTM Reference: MU9959

Site 2 was located in a slough surrounded by a cypress swamp on the south side of Tamiami Trail (US 41) on a privately owned property known as "Leon's Orchid Isles" in Collier County (Fig. 5). Orchid Isles is located on US 41, 18 miles east of Ochopee and 4.7 miles east of Monroe Station and approximately 5 miles west of Fifty Mile Bend. The study area was in a slough in Gator Hook Strand which received drainage from the Tamiami Canal and the Big Cypress Swamp. Water flow was from north to south from Big Cypress to the Tamiami Canal and into Gator Hook Slough. Flow rates varied seasonally and were dependent upon precipitation and water management practices. Data were collected near the bridge passing over the slough.

The hermit who owned the property would not allow spray crews to treat the plants with herbicides. Hence, it seemed to be an ideal spot for a long term study. Both Neochetina elichhorniae and N. bruchi were common as were most other insects, mites, and pathogens. Sameodes albiguttalis was released at the site in June and July 1978 and efficacy studies were begun in September.

Site 3: Everglades Conservation Area 3A
UTM References: NU5483, NU4383, and NU3861

Site 3 was comprised of three study areas, designated 3A, 3B, and 3C, located in Everglades Conservation Area 3A (Fig. 6). Movement of water through this area is generally from north to south and is supplied by rain and runoff from agricultural land located north of the conservation area and south of Lake
Figure 5. A map of the location of site 2 at Leon's Orchid Isles in Collier Co. within Big Cypress Swamp. The inset shows the location of the site in relation to Monroe Station and the county lines. The numbers within the site represent sampling stations.
Figure 6. A map of the Everglades Conservation Areas showing the locations of sites 3 (A, B, and C) and 7.
Okeechobee. The water level is dependent on seasonal rainfall but is controlled by the South Florida Water Management District. Normal water flow in the canals is outward to the ocean but flow rates and direction are also controlled by S.F.W.M.D. pumping.

Site 3A (Fig. 7) was located in Broward County at Everglades Holiday Park in an airboat trail on the north side of the South New River Canal and the east side of Canal L68A approximately one mile west of U.S. 27 and four miles south of S.R. 84 (Alligator Alley). At the site, water flows from north to south through the conservation areas, then drains into the South New River Canal which flows east to the Atlantic Ocean.

Site 3B, also located in Broward County, was on the west side of the Miami Canal approximately 2 miles north of the intersection of the Miami Canal and the South New River Canal (Fig. 8). The Miami Canal flows in a generally southward direction from Lake Okeechobee to just north of the Broward County line where it flows southeast through the Everglades Conservation Areas, and into Miami where it joins the Miami River and flows into Biscayne Bay. The South New River Canal flows east from the Miami Canal and eventually to the ocean.

Site 3C was located in Dade County on the west side of L-67A in the marsh between earthen mounds (spoil banks) which border the west side of the canal approximately 5 miles north of U.S. 41 (Fig. 9). Canal L-67A runs southwest from the South New River Canal to the Tamiami Canal. The water flows southwest and is supplied by the South New River Canal, partially by the Miami Canal, and drainage from the surrounding wetlands.

Site 4: Lake Alice

UTM Reference: LC 6980

Site 4 was the last of the 20 original Sameodes release sites. It is
Figure 7. A detailed map of site 3A showing the sampling area off of the main channel and behind a levee which resulted in very restricted water flow patterns.
Figure 8. A map of site 3B in which the sampling area was located in an airboat trail between two spoil banks. The plants in this area were very much under the influence of flow from the adjacent Miami Canal.
Figure 9. A detailed map of site 3C which was located at the very edge of a canal, behind a berm, and between two spoil banks. As a result, the plants in this area were influenced more by sheet flow from the grass flats northwest of the site than by the channelized flow of water through the canal. An extensive fringe of hydrilla along the canal bank also tended to impound this site.
Located in Alachua County at Lake Alice, a 33 ha. lake on the University of Florida campus in Gainesville. The water to the lake is supplied by effluent from the University sewage treatment facility, rainfall, runoff, and overflow from Hume pond, a small sinkhole at the northeast end (Fig. 10). Water flows from east to west. Discharge is through deep well injection at the western end. A catwalk and fence divide the lake into 2 parts (Fig. 11). East of the catwalk, approximately 20 ha. of the lake is covered by a marsh. The remaining 13 ha. of Lake Alice west of the catwalk is open water. The average depth of the lake is 1.3 m. while that of the marsh is 0.5 m. Data were collected at regular intervals on the east side of the catwalk. The catwalk's supporting posts were numbered from 1-50 starting with #1 at the north side of the lake. Data were collected at posts 8, 18, 28, 38, and 48 at each observation. Biomass samples were collected at posts 8, 13, 18, 23, 28, 33, 38, 43, and 48.

Site 5: Lake Manatee

UTM References: LA7142 and LA6740

Lake Manatee is a man-made reservoir located in Manatee County approximately 15 miles east of Bradenton. The main water supply for Lake Manatee is the Manatee River which flows in a generally westward direction from Tampa Bay. The Manatee River flows into Lake Manatee at its northwest side and out at the lake's southeast end. Lake Manatee also receives water from numerous creeks to the north of the lake, the largest ones being Gilley Creek at the northeast end of the lake and Boggy Creek at the northwest end. Data were collected from two areas which were designated 5A and 5B (Fig. 12).

Site 5A was located on the northeast end of Lake Manatee in Gilley Creek at the junction of Rt. 675 and Rt. 64. Gilley Creek, which flows southwest, empties
Figure 10. A map of Lake Alice in Gainesville, Alachua Co. The study area was on the marsh side of the catwalk. Flow was in a generally east to west direction from the university sewage treatment facility and Hume pond to the discharge wells.
Figure II. A detail of the sampling area showing the catwalk with every fifth piling (black dots). The transect was parallel to the catwalk and the sampling points corresponded with the piling numbers. For example, point 38 was the 38th piling from the north end. The marsh in this area was comprised mainly of waterhyacinth and Hydrocotyle spp. with Typha sp. near the shoreline.
into Lake Manatee at the north side of the east end of the lake. The creek's water source is from other smaller creeks which empty into Gilley Creek, rainfall, and runoff. The data were collected from the east side of the Rt. 675 bridge which crosses Gilley Creek.

Site 5B was located near the boat ramp on the south side of Lake Manatee in Lake Manatee State Recreation Area. The park is located south between the lake and Rt. 64.

Site 6: Occidental Chemical Corporation

UTM Reference: LD2963

Site 6 was located in Hamilton County, 4 miles northwest of White Springs, Florida (Fig. 13). The site was a phosphate mine in a land reclamation area of the Occidental Chemical Company (Oxy), Suwannee River Complex, located 15 miles northwest of Lake City at Rt 137. The mining pit had an irregular shape with finger-like projections in all directions (Fig. 14). The area and shape of the lake on the southeast side were constantly changing because of mining in that area. Groundwater was the main supply of water to the lake through mining operations. Drainage from the surrounding barren land and direct rainfall also supplied water to the lake. Water level was controlled by seasonal changes and pumping from the lake northward through the culvert on the north side into a canal.

The site was #260 in the S. albuguttalls dispersal study. Since the lake covered such a large area and different waterhyacinth types could be found from one area to another, the lake was divided into three general observation areas: 6A, located on the west side nearest the office buildings; 6B, located on the north side at a spillway and road culvert; and 6C, located on the east side near
Figure 13. A map showing the location of site 6 at the Occidental Chemical Company northeast of White Springs in Hamilton Co.

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Figure 14. A detail of the quarry at Occidental within which extensive waterhyacinth mats (dark areas on map) occurred. The locations of the three sites are shown.
where the Oxy crews were mining at the time. The south side was not easily accessible and was located in the mining area so a study site was not established there.

Site 7: Everglades Conservation Area 2A

UTM Reference: NV5401

Site 7 was located in Conservation Area 2A of Broward County approximately 7 miles north of S.R. 84 (Fig. 15). Data were collected from a marsh east of U.S. 27 and the North New River Canal 0.3 miles south of 26 mile bend at Sawgrass Recreation Area (see Fig. 6). Water normally flows from Lake Okeechobee south through the North New River Canal and Conservation Area 2A to S.R. 84 then east to the Atlantic Ocean. During times of flood conditions, usually during a hurricane, the water flow is controlled by S.F.W.M.D. and is pumped north to Lake Okeechobee. Water is supplied by Lake Okeechobee, agricultural runoff north of the site, and rainfall. Water level changes with seasonal precipitation.

A continuous fringe of waterhyacinth extended from the west bank of the canal. The east side of the canal did not have a well-defined bank but was Everglades marsh. The waterhyacinth mats were growing in open areas between stands of cattail. In the middle of the canal there was an island of cattail and waterhyacinth. The waterhyacinth shoots were small with inflated petioles. Shoots were tagged along the fringe on both sides of the canal and on the fringe of plants extending from the island. South Florida Water Management District agreed to cooperate and the locations of the sites were marked with red flags to alert spray crews to avoid spraying the area.
Figure 15. A map showing the location of site 7 in Everglades Conservation Area 2A, near the Sawgrass Recreation Area in Broward Co. The waterhyacinth population was in a canal which ran parallel to U. S. 27. See also Fig. 6.
Site 8: Snake Creek

UTM Reference: MB8386

Site 8 was located in Volusia County along Snake Creek, an approximately one mile long creek which is part of the St. Johns River chain. A site on the St. Johns River was desired but the main river channel was sprayed with herbicide frequently so the little creek north of the main flow seemed to be a good study site. The site was located ca. 6 miles east of Sanford and 4 miles southeast of Lake Monroe (Fig. 16). The river chain flows generally from south to north but at this point the St. Johns and Snake Creek flow from east to west. The main water supply for the St. Johns at the study site is from Lake Harney located to the southeast. Snake Creek's water is supplied mainly by Thornhill Lake and Hickory Slough which are supplied by the St. Johns River. Water is also supplied by runoff from the surrounding cow pastures. Snake Creek flows into the St. Johns River and this water then flows into Brickyard Slough then northwest into Lake Monroe. The water is high in nutrients from the agricultural drainage. Water level is dependent on the seasonal precipitation.

A fringe of small waterhyacinth shoots extended to ca. 1.5 meters from the creek's banks. The fringe was not continuous but was comprised of variously sized mats along the banks. Fifteen waterhyacinth shoots were tagged ca. 30 meters apart along this fringe. A red flag was stuck into the rhizome of a waterhyacinth shoot near each of the tagged shoots to mark the location and to alert spray crews to the research site. An airboat was used to reach the site but a small rowboat was used for working in the waterhyacinth mats.

Site 9: Lake Okeechobee

UTM References: MW9481 and NV1798

Lake Okeechobee is located centrally in south Florida and is the second
Figure 16. A map of the St. Johns River in the vicinity of Lake Monroe and Lake Jessup showing the location of Snake Creek and site 8.
largest freshwater lake in the United States. The lake is used as a reservoir in times of flood and is surrounded by a 25 foot dike and a system of canals managed by the U.S. Army Corps of Engineers and the South Florida Water Management District. The lake measures approximately 35 miles long by 30 miles wide and covers an area of 448,000 acres.

Water flows from north to south in Lake Okeechobee and is supplied primarily by the Kissimmee River and its tributaries which empty into the lake at the northwest bank. Lake Okeechobee also receives water by drainage from Taylor Creek at the north end, Nubin Slough at the northeast bank, Lettuce Creek and Hendry Creek at the east bank, Nicodemus Slough at the west bank, drainage from the Lake Istopoga basin and the surrounding area (mostly agricultural), and direct rainfall. In its natural state, Lake Okeechobee had no outflows until the man-made drainage and canal system was implemented. Sheet flow from overflow at the south end of the lake formed the Everglades and originally discharged eventually into Florida Bay and the Gulf of Mexico.

Site 9 was comprised of two locations in Lake Okeechobee which were designated as 9A and 9B (Fig. 17). Site 9A was located in Glades County approximately at the midway point on the west side of Lake Okeechobee in Fisheating Bay. The data were collected from an area south of a chain of islands called the "Spoil Islands." These islands extend out into the open water of Fisheating Bay. The site was located on the south side of the eighth island from the east. From the north, the Harney Pond Canal empties into Fisheating Bay and the site was located at the fourth island east of that canal approximately 5 miles from the "Sportsman Village" located at route 78.

The waterhyacinth were unprotected in the open water of Fisheating Bay so the study was moved to a new site, 9B, in the north end of the lake.
Figure 17. A map of Lake Okeechobee showing the location of site 9A at the mouth of Fisheating Creek and site 9B on the eastern side of King's Bar Island.
Site 98 was located in Okeechobee County 8 miles south of Okeechobee City. The location of the study area was near the North Lake Shoal by King's Bar Island which was ca. 3.25 miles long and partially covered by aquatic vegetation, and was located 1 mile to the southeast of the Kissimmee River. Data were collected on the east side of the island approximately 3 miles from the mouth of the Kissimmee River. The adjacent shoal was covered by water 3 to 5 feet deep except during times of drought when it was completely dry.

Site 10: St. Johns River
UTM Reference: MC6407

Site 10 in Lake County was located at the south bank in the north end of an oxbow of the St. Johns River at the point where the oxbow joins the main river channel at channel marker 41 approximately 3 miles west of Deland and 1 mile south of the Rt. 44 overpass at Deland Landing Park (Fig. 18). The natural river course serves as a boundary between many counties and, at this point, the river divides Lake County to the west from Volusia County on the east.

The origin of the St. Johns River is the St. Johns marsh located in the southwest area of Brevard County. It is a 273 mile long river which flows from south to north and eventually empties into the Atlantic Ocean at Jacksonville. Water is supplied by numerous lakes, rivers, creeks, swamps, and drainage from agricultural land. For approximately one third of the St. Johns length from its origin to Lake Monroe, the river is small and meanders through swamps, marshes, and pasture land. It flows into Lake Monroe at the northeast end and out at the west end. Here the St. Johns becomes well defined and is under tidal influence. Site 10 was located approximately 14 miles northwest of Lake Monroe.

The main water supply to the St. Johns River in the area of site 10 is
Figure 18. A map of the St. Johns River on the border between Lake Co. and Volusia Co., near DeLand showing the location of site 10.
Shell Creek and Mud Lake which flow into the river 0.5 miles south of the site. The Wekiva River flows into the St. Johns River 8.5 miles south of site 10. At the site, water flows from east to west then joins with the main river channel and flows north once again. Water level varies seasonally with precipitation.

Site 11: Coral Springs

UTM Reference: NV7606

Site 11 located in north Broward County (Fig. 19) was #313 in the Sameodes albiguttalis dispersal study. Data were collected from 2 experimental evaporation ponds at the City of Coral Springs Waste Water Treatment Facility (Fig. 20) located approximately 2.5 miles west of U.S. 441. The two data collection sites are referred to as 11A and 11B.

At the waste water treatment plant there are five oblong asphalt ponds each approximately 2 feet deep. They all were completely covered with waterhyacinths which were used experimentally to remove high nutrient concentrations from sewage effluent. A canal parallels the west side of the facility. The southeast pond is the largest of the five and covers an area approximately twice the size of the other four. The southeast pond is used for research by various state and federal groups and the waterhyacinths may remain there for up to a year before being harvested. The four smaller ponds are used by the City of Coral Springs and are harvested biweekly leaving only a small fringe of plants which grow and cover the entire pond in two weeks time. Site 11 was located at the west end of the southeast pond approximately 10 feet from the west side.

Four evaporation ponds are north of the asphalt ponds along the west side of the facility. Treated effluent was pumped into these ponds and allowed to evaporate and seep into the ground. Site 11B was located on the west side of
Figure 19. A map of the Palm Beach Co. area showing the locations of sites 11, 14, and 15.
Figure 20. The layout of the ponds at the Coral Springs Sewage Treatment Plant showing the two study sites I1A and I1B. Site I1A was in a series of ponds through which treated wastewater was circulated in an experiment to test waterhyacinth for tertiary treatment and nutrient removal. This lagoon was the first to receive the wastewater at the western end and it was then circulated anti-clockwise to the other ponds. Site I1B was a settling pond for the treated sewage. The two types of shading at I1B show the increase in waterhyacinth coverage from October to November 1981.
the second pond beside the canal north of the asphalt ponds. The data were collected at 10 replicate areas ca. 2 m apart from the west bank towards the northeast for ca. 10 m to the fringe of the waterhyacinth mat. Three replicates were placed along the edge towards the north and two were placed towards the northwest.

Site 12: Lake Trafford

UTM Reference: MV5222

Site 12 was located in Collier County on the southwest side of Lake Trafford 3 miles west of Immokalee (Fig. 21). Water is supplied to Lake Trafford mainly by the Corkscrew Swamp and direct rainfall but also receives drainage from urban Immokalee through a canal which empties into the lake at its east bank. Water flows from north to south in the 1494 acre lake and drains into the surrounding swamp. Water level varies seasonally with precipitation.

Lake Trafford has a variety of aquatic plant growth. Waterhyacinth and hydrilla cover most of the lake. Large waterhyacinth mats grow along the perimeter of the lake and some of these, which are acres in size, are in open water while others are on top of hydrilla. The plants are of various sizes from small lush plants to tall spindly chlorotic ones. The waterhyacinth at Lake Trafford is frequently treated with herbicide by the U.S. Army Corps of Engineers and S.F.W.M.D.

In August 1981, an area on the southwest end of Lake Trafford was chosen as research site 12. A fringe of waterhyacinth extended from the lake's surrounding swamp. However, the small, young shoots were closest to the bank (swamp) and the taller, older, spindly shoots were on the outer edge of the mat. The site could have been an old herbicide plot which would explain why the younger plants were located near the bank and not on the outer fringe.
Figure 21. A map of the Immokalee Area in Collier Co. showing the location of Lake Trafford and site 12.
Site 13: Wekiva River

UTM Reference: MB7858

Site 13 was located on the Wekiva River 2 miles northeast of Wekiva Springs and 6 miles northeast of Apopka (Fig. 22). The Wekiva River's main water sources are Wekiva Springs and Rock Springs. The headwaters of the river is Wekiva Springs. The swiftly moving Wekiva River flows eastward for slightly more than one mile then northward where it joins the St. Johns River ca. 11 miles north of site 13. Rock Springs is located ca. 4 miles north of Wekiva Springs. Rock Springs Run flows north from the springs then south into the Wekiva River ca. 1 mile east of Wekiva Springs. Water is also supplied by various creeks, drainage from the surrounding forest, and direct rainfall. The cool 23°C water is clear and mineral rich from its originating springs.

Data were collected from waterhyacinth mats extending from both banks of the Wekiva River according to the procedures described as 7, 8, and 9. At the study site, the river flows between Orange County on the west bank and Seminole County on the east.

Site 14: West Palm Beach

UTM Reference: NV8559

Site 14 was located in Palm Beach County on West Palm Beach City property in Canal M, 2.5 miles west of the populated area of the city of West Palm Beach (see Fig. 19). The canal flows through Loxahatchee Slough which is the main water supply to Canal M at site 14. Data were collected in the canal ca. 0.5 miles west of the Florida Turnpike. This canal is a principal source of water for West Palm Beach. Water flows from west to east and originates at Lake Okeechobee. At the east side of Lake Okeechobee water drains east into Canal
Figure 22. A map of the Wekiwa Springs State Park Area showing the Wekiwa River and the location of site 13.
L-8 then flows through L-8 southeast receiving drainage from agricultural land until it joins with Canal M where it flows east to the West Palm Beach water treatment facility and into reservoirs.

**Site 15: Cypress Creek Canal**

UTM Reference: NV8201

Site 15 was on the Cypress Creek Canal at the Palm-Aire community just east of the Florida Turnpike near Pompano Beach (see Fig. 19). The Cypress Creek Canal originates 2.7 miles west of the site where it is joined by the C-14 Canal. C-14 originates 17.5 miles west of the site at the North New River Canal at US.27. From U.S. 27 the water flows northeast for approximately 4 miles then east and eventually out to the ocean. During hurricanes and flooding, the water is pumped to Lake Okeechobee. Water to the canal is supplied by drainage from conservation area 2A north of C-14 Canal and is dependent on seasonal rainfall and management practices.
RESULTS

Site 1: Sawgrass Lake, Pinellas County

This site was near the original *S. albiguttalis* release site #2. Initially, examinations indicated that *S. albiguttalis* had not become established here, but, in June 1978, three larvae and one pupa were found near the release site. In August, an infestation of *S. albiguttalis* was found near the road culvert at Rt. 600 in a drainage canal used for control of surface runoff. More *S. albiguttalis* larvae were found in the small plants near the culvert than elsewhere. These plants typically bore leaves with the inflated type of petiole (see Fig. 1). The waterhyacinth population initially was comprised of small shoots near the culvert and graded into large shoots downstream towards the lake.

Data collected in September 1978 indicated that *S. albiguttalis* damage was extensive only on the fringe of plants nearest the road culvert (Fig. 23). Examination of plants collected at random, showed 70% of the shoots and 23% of the total leaves damaged by *S. albiguttalis*. *S. albiguttalis* larvae were only found within 25 m of the culvert. Conditions remained about the same in October 1978, with the *S. albiguttalis* activity still limited to the west end of the canal.

New leaves produced during October had given the mat a healthy appearance and older leaves, which previously showed symptoms of fungal infection, were below the canopy of new leaves. In December, the growth of plants had slowed and leaves infected by fungus were again noticeable in the canopy. Average height of plants had decreased from 59 cm in September to 48 cm in November (Fig. 24). Plant density at station #1 averaged 108 plants per square meter in
Figure 23. The percentage of waterhyacinth shoots with injury caused by feeding of *S. albicipitalis* larvae at site 1 and various sampling points at 10 m intervals down the canal. The periods designated "washout" indicate that large volumes of water rushed through the canal and tended to push the plants downstream towards the lake thus partially or completely clearing out the canal.
Figure 24. The height of the plant canopy as measured by the length of the third position leaf cohorts along the canal transect.
October and had increased to 160 by November (Fig. 25). Shoots damaged by *S. albiguttalis* increased from 10% to 80% within the same period of time. Aerial photographs show the waterhyacinth mat at station #1 was disturbed by high water flow from the culvert and plants along the first 30 meters of the north bank were washed away. By mid-December newly produced shoots had filled in the open water surface area and the water was low with portions of the canal bottom exposed. Damage by *S. albiguttalis* decreased from 80% in November to 10% in December because older damaged leaves had been replaced by new growth with no subsequent reinfestation of *S. albiguttalis*.

By January 1979 most of the plants within the study area had been pushed down the canal into the south end near the lake by high water. Only fragments of the waterhyacinth mat remained along the bank. Plants and debris that were originally at the road culvert were found near station 8 which was the only area where *S. albiguttalis* damage was observed. Most of the small plants had been washed into an area beyond the sampling stations. Plants along the canal bank within the sample area were jumbled and the taller plants had fallen over due to a lack of adjacent plants for support.

By February 1979 new shoots had been produced along the bank from remnants of the fragmented mat. These shoots bore leaves with inflated petioles and were dark green. Leaf length decreased from January to February (Fig. 24) as the lower density caused the taller plants to produce smaller leaves. In many cases, these larger plants had also produced new offshoots. Sample area #3 had only a fringe of small plants along the bank. Populations of *S. albiguttalis* were low and plants sampled showed no signs of *S. albiguttalis* damage.

During March and April 1979 shoot density had begun to increase. In March *S. albiguttalis* damage was detected only at stations 6 and 8 (see Fig. 23).
Figure 25. Variation in plant density in terms of shoots per square meter at different locations along the transect and on different dates.
However, in April *S. albivittalis* larval damage was apparent at all sample stations.

During May 1979 heavy rains (17"), and 2 breaks in sewer mains flushed most of the plants from the canal into Sawgrass Lake (see Fig. 26). Rushing water also undermined the wall of concrete bags used to stabilize the north bank. This resulted in the collapse of the wall. By July 1979, plant density (Fig. 25) had recovered and averaged 114 shoots per square meter. Most of these were along the south bank of the canal and existed as a small fringe of plants. Also, by this time *S. albivittalis* damage had increased and ca. 52% of the shoots along the transect were damaged (Fig. 23). *Neochetina* spp. increased also, as the percentage of leaves damaged was 87% in July (Fig. 27).

In summary, activity of *S. albivittalis* along the transect was apparent beyond station #6 until the waterhyacinth mat was washed out by flooding. As regrowth began in the canal and plants bearing leaves with inflated petioles predominated, *S. albivittalis* numbers generally increased. The percentage of both shoots and leaves damaged decreased as canopy height increased.

The first study was terminated in July 1979, because of the disruption of the site. Because conditions at the site had changed, the original objective of monitoring the dispersal of *Sameodes* movement over a stable mat was no longer appropriate. However, since *S. albivittalis* and *Neochetina* spp. populations had increased and were well established in the newly forming waterhyacinth mats, a second study was initiated in August 1979 to determine if they could restrict the growth of the developing mat.

During the second study data were collected along the edge of the growing waterhyacinth mat. The canal was periodically surveyed and the waterhyacinth coverage mapped according to the methods described in procedure 4 to determine
Figure 26. Maps of the section of the canal leading into Sawgrass Lake which show waterhyacinth coverage on subsequent dates within the study area. After the May washout the canal was not completely covered again for nearly eight months. This unusually long period of regrowth was largely due to the inhibitory effects of _S. albiguttalis_.

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Figure 27. A 3-dimensional graph showing the percentage of leaves injured by adult Neochetina spp. feeding at the various sampling stations in the canal and on various dates.
the extent of mat development over time. Both aerial and ground level photographs were periodically taken to aid in the mapping and measurement of mat growth.

Fig. 26 shows the maps of the section of canal under study as it appeared at monthly observations. Coverage increased at a nearly constant rate (ca. 12% of the total area per month) from May 1979 until December 1979. During this 7 month period coverage increased from nearly 0% in May to ca. 95% in December.

*S. albiguttalis* activity varied among sampling locations and was dependent upon the type of plants present along the fringe. Damage increased from 60 to 100% of the shoots at station #4 between August and September (Fig. 28). New shoots produced were small and the damage decreased to 43% and 15% at this location in October and November, respectively. In December the larval population increased again and 100% of the plants showed signs of *S. albiguttalis* feeding damage. The mat was sparse at stations 1, 2, 4, and 5 in December and these were the last areas to fill in. Plants in these areas bore small leaves ranging in length from 14 to 22 cm with inflated petioles. At station #2 in January 1980, 85% of the shoots examined were damaged by *Sameodes*. All of the damage was type A ("window") damage (Figs. 29 and 30).

In February 1980 the taller leaves of older shoots had been damaged by frost. Leaves on small plants beneath the canopy remained dark green. Water level was approximately 3 feet higher than noted at previous observations. Older plants had produced leaves which were slender and erect. The "windows" produced by *Sameodes* were found only in the older leaves, which were beginning to die. Small, healthy, dark green plants were found at station #1 where all of the shoots examined were heavily damaged by *S. albiguttalis* larvae with the youngest leaf missing on some. Fourth and fifth instar larvae were found within the stem apices.
Figure 28. The percentage of shoots injured by *S. albifasciatus* larval feeding at various sampling locations within the canal and on subsequent dates. This represents data from the second study conducted at this site. This should be contrasted with Fig. 23.
Figure 29. Data from August 1979 to September 1980 illustrating a temporal change along a 100 m transect in the percentage of waterhyacinth shoot injury resulting from the feeding activity of early instar *S. albiguttalis* larvae (type A damage).
Figure 30. Same as Figure 28 but data represent the percentage of shoots injured by late instar *S. alboguttalis* larvae (type B damage)
EFFICACY OF SAMEODES ALBIGUTIALIS AS A BIOCONTROL OF WATERHYACINTH (U) ARMY ENGINEER WATERWAYS EXPERIMENT STATION VICKSBURG MS ENVIRONMENTAL LAB

UNCLASSIFIED T D CENTER ET AL. JAN 84 WES/TR/A-84-2 F/G 6/6 NL
Observations in April 1980 indicated that adult *Sameodes* were abundant and nine adults were observed between sample stations 1 and 3. The waterhyacinth mat was extremely dense and *Neochetina* spp. populations were higher than at previous observations. Examination of plants in sample area #5 revealed that at least 20% of the stem apices were damaged by *S. albiguttalis* larvae and stress caused by a combination of *S. albiguttalis* and *Neochetina* spp. feeding had stunted the plants. Numerous shoots had produced malformed spindly leaves. Damaged shoots had produced offsets which were in turn also attacked by *S. albiguttalis* larvae. The furled newly emerging leaves on many shoots had wilted before they had a chance to open because of damage caused by *S. albiguttalis*. Shoot density varied among sample stations. Plant height and color appeared to be similar throughout the canal except for the one area near sample #5 where plants were smaller and more heavily damaged.

Percentage of shoots damaged by *S. albiguttalis* larvae (averaged over all stations) began to decline in April (see Fig. 31), but the percentage of shoots with lethal damage increased. Figure 31 shows the "trade-off" between A and B damage that began during this period. Leaf length averaged 41 cm and the shoots were beginning to become quite tall (Fig. 32). Type A damage was most prevalent in inflated type petioles which the plants lost as they became taller and as density increased.

Leaf length averaged 66 cm in May and ranged from 56 to 82 cm with the smallest plants at stations 1, 3, 5, and 8 (Fig. 32). These were the last areas of open water to close in. By August leaf length had increased greatly at station #1 but a fringe of plants was always present at the mouth of the culvert. This was the only area where damage by young larvae (Type A) was evident (see Fig. 29). By late summer all types of *S. albiguttalis* damage had become sparse.
Figure 31. A comparison of type A and type B injury to waterhyacinth shoots caused by *S. albiguttalis* larvae averaged over all transect points by date as compared to the total percentage of shoots damaged. Note that until April 1980 type A damage was prevalent but during the summer type B damage was prevalent. The transition corresponded with the period during which the canal was completely covered and the shoots were quite tall. Also note that the data for September 1979 and 1980 were nearly identical.
Figure 52. The height of the waterhyacinth canopy as measured from the water surface to the uppermost leaf layer at various transect points from November 1979 to September 1980. Note the increase in height at all points in May 1980 which persisted until the washout in late summer.
By May plants had almost completely covered the canal and all had weevil feeding damage. Plants appeared to be outgrowing the effects of Sameodes at station #4. Shoots bearing leaves with inflated petioles were absent at most stations except for an area of ca. 3x7 m east of station #5 which was the only location with open water. Even there, only a few plants with inflated petioles were present. These petioles, however, bore extensive larval damage which was evident as large petiole windows visible from several feet away. Red spider mite damage was not as extensive as it was in April. Many of the young, position 1 leaves were severely damaged by S. albiguttalis larvae and had wilted. Examination of shoots revealed many position 2 leaf petioles damaged by Sameodes larvae which had not yet wilted. Fourth and fifth instar larvae were predominant. At least 29 S. albiguttalis adults were seen including 12 near station 5.

In July, the plants had changed little. Only a few plants with inflated petioles were found and these were near the road culvert. Water depth at station #1 was only 45 cm. A. zonatum was apparent on most of the older leaves. Only a few of the plants had signs of lethal damage. Some of the large shoots had begun to sink and the rhizomes were submerged. Neochetina spp. adults had fed heavily on these plants with as many as 700 feeding spots on some leaves.

By August, plants near the road culvert had been sprayed with herbicide and samples were collected near the bank in an area that had not been treated. Neochetina spp. feeding damage appeared to have increased. One shoot examined had 12 adult weevils of which 8 were N. bruchi. Another shoot examined near station 8 had 14 weevils in the wrapper leaf, three of which were N. bruchi. Leaves older than the 3rd position had been heavily damaged by A. zonatum and plants with inflated petioles were present only in the area that had been treated with herbicide. Plants damaged by S. albiguttalis were few. Lethal
damage was found at most stations but steadily declined from 38% in May to only 7% in August.

By September the plant coverage decreased by ca. 50% due to flooding. Waterhyacinth coverage was sparse in the vicinity of the sample stations. Plants that were originally in the study area had been washed into the lake. Data were collected on plants at each station and *S. albiguttalis* was found to have damaged 68% of the shoots examined but most of the damage was "window" type (type A).

**Site 2: Leon's Orchid Isles**

This site was originally chosen because it was known to be well protected from herbicidal control operations and because it was known to have persisted for several years. This was one of the original *S. albiguttalis* release sites (site 5 of Center, 1981a) as well as near an original release site for *Neochetina bruchi* (ca. 1974). Overall, this site was found to be very stable and therefore not amenable to *S. albiguttalis* infestation. This was the first site, however, where the very distinct spatial organization of various insects, mites, and pathogens on the shoots became apparent.

Fig. 33 illustrates various morphometric features and population characteristics of the waterhyacinth population present at this site. These data represent observations over a period of 17 months beginning in September 1978. Canopy height varied from ca. 40 cm to nearly 70 cm, becoming taller in the summer and fall and shorter in the winter. Root length ranged from ca. 25 to 35 cm with almost no seasonal pattern to this variation. It is curious that plant size was smaller during the fall of 1978 than during the following fall as evidenced by a lower canopy height as well as shorter roots.
Figure 33. Morphometric measurements and population characteristics of the waterhyacinth mat at site 2. Canopy height and root length are plotted on ascending and descending axes, respectively. Note that seasonal fluctuations were relatively minor and that this represents a very stable population.
Standing crop varied from ca. 0.8 kg/sq m in the winter to ca. 1.8 kg/sq m by late fall. This seasonal range of only 1 kg is typical of sites with very mild winters and situations where perturbations on the plant population are few and relatively minor.

Although this was a release site, *S. Albiquuttalis* populations did not become established within the study area. Large numbers of larvae were found on the opposite site of the road on plants in the Tamiami Canal, however. Repeated sampling as well as extensive examination of shoots not included in the sampling procedure failed to produce specimens within the sampling area although signs of *S. Albiquuttalis* larval damage were apparent from time to time. In January 1979 *S. Albiquuttalis* larvae were found on small, inflated leaf petiole type shoots at the periphery of the study area just south of the bridge. This area was affected by a herbicide overspray from crews treating the Tamiami Canal and these plants were representative of the regrowth present there. As such, they were very different from the plants in the unsprayed area being much smaller and more robust. Only one larva was found before we decided to avoid further disturbance of the population and stopped searching.

*Neochetina* spp. adults and larvae were common within this site and were consistently present and ubiquitous. Weevil adult feeding lesions were present on nearly every shoot and, in fact, on almost every leaf. Larvae varied more in frequency of occurrence both in terms of seasonal and intra-shoot distribution. Fig. 34 illustrates the proportion of each of the leaf cohorts which bore signs of *Neochetina* larval injury. In June 1979, a large proportion of the young leaves (cohorts 1 to 6) were damaged by weevil larvae. This proportion decreased through late October after which it increased somewhat in November and December only to decrease again in January. Generally, however,
Figure 34. The percentage of leaves grouped by leaf position cohorts (with cohort one representing the youngest leaves) injured by the feeding activity of Neochetina spp. larvae. Note that damage to young leaves is temporally variable and relatively uncommon. The shaded portion represents leaf cohorts that were dead, primarily due to senescence.
the greatest frequency of larval damage was to the older leaves. This was undoubtedly due to the greater cumulative effect of subsequent attacks over the life of the leaf.

Waterhyacinth mite (Orthogalumna terebrantis) galleries were present every month except January 1980 (Fig. 35). During June, late August, and November signs of leaf injury were apparent on young leaves (those less than cohort 7). During early August and October damage was restricted primarily to the older leaves. In December mite injury was very low on all leaf positions, and by January it was undetectable.

Zonate leaf spot (Acremonium zonatum) lesions seemed to have a frequency of occurrence similar to that of O. terebrantis. Its occurrence on young leaves was rare, however, especially on those of the fourth position or less (Fig. 36). Lesions occurred at high frequencies on older leaves throughout the study (June to January).

Spider mites (Tetranychus urticae) showed almost no intra-shoot spatial pattern (Fig. 37). In early October high frequencies of spider mite injury were apparent on old leaves. By late October this had shifted to high frequencies on young leaves. During November the outbreak progressed to all leaves within the population regardless of age. The infestation declined in December and was barely evident in January.

The frequency of leaf injury caused by the pickerelweed borer (Arzama densa) also failed to exhibit an intra-shoot spatial pattern (Fig. 38). Leaves in all positions showed signs of injury in the summer but frequencies were never high. The position of injured leaves increased throughout the remainder of the year suggesting that the old damaged leaves were displaced by new leaves which were not subsequently re-infested by A. densa larvae.
Figure 35. The data for waterhyacinth mite (Orthogalumna terebrantis) injury to waterhyacinth leaf cohorts represented over time.
Figure 36. Data for incidence of zonate leaf spot (Acremonium zonatum) injury on leaf cohort groups presented as in Figs. 34 and 35.
Figure 37. Data for incidence of spider mite (Tetranychus urticae) injury presented as in Figs. 34-36.
Figure 38. Data for the incidence of injury caused by the pickerelweed border (Arzama densa) larva on water-hyacinth leaf cohorts presented as in Figs. 34-37.
Figs. 39 and 40 show the trends for the frequency of occurrence of injury by various biological control agents to waterhyacinth shoots. In this case, if signs of injury were present on any leaf on the shoot, then the shoot was considered damaged by the particular agent. Certain factors, weevil adults and zonal leaf spot in particular, were always present on nearly every shoot. This was also true of weevil larvae although frequencies decreased in the winter to a greater extent than the others. Spider mites, waterhyacinth mites, Arzama, and S. albigitalis were seasonal. Shoot injury by Arzama peaked in early August, that caused by Sameodes peaked in early October, and spider mite injury peaked in late November. Injury caused by waterhyacinth mites occurred frequently in June, decreased somewhat through the summer, peaked again in October, then decreased to negligible amounts by January.

Data from this site include counts of numbers of weevil adults and larvae, A. densa larvae and pupae, and S. albigitalis eggs, larvae, and pupae. As noted earlier, S. albigitalis was not found in the study area, nor were A. densa pupae. The data on A. densa larvae and the weevil larvae and adults are shown in Fig. 41. This illustrates a seasonal pattern for the weevil infestation that would otherwise not have been apparent. Neochetina larvae showed periods of peak abundances in the spring and fall. Adults, although unexplainably low in 1978, showed three distinct peaks (which probably correspond with generations) as the population increased in 1979. The first peak occurred in March, the second three months later in June, and the third three months later yet in September. Adult populations peaked at ca. 2 individuals per shoot in September.

As can be seen, A. densa larvae were never abundant, certainly not as abundant as the frequency data indicated.
Figure 39. The relative frequency of waterhyacinth shoot injury caused by A. densa larvae, spider mites, or S. albifolialis larvae from June 1979 to January 1980. These data differ from the previous data in that any damage on any leaf of a shoot is counted as injury to the shoot.

Figure 40. The relative frequency of waterhyacinth shoot injury caused by Neochetina spp. adults and larvae, waterhyacinth mites, and zonata leaf spot.
Figure 41. Monthly data from September 1978 through January 1980 which show relative numbers of *A. densa* larvae and *Neochetina* spp. adults and larvae at site 2. The data presented as number per 100 shoots examined.
In summary, although *S. albiguttalis* was never an important factor at this site, several bits of information were gained. First, it was learned that *S. albiguttalis* would not infest some types of waterhyacinth populations. Second, it was realized that to really gain insight into the factors that affect waterhyacinth plants the spatial distribution of the factors on the shoot must be studied. It is not enough to merely count damaged leaves, for example. Some leaves are more critically important to the plant than others. Third, the most important lesson was that the plant can affect the spatial distribution of its natural enemies through variable rates of leaf production and leaf production rates must therefore also be a part of any biological control assessment. The cumulative effect of all leaf mortality agents on the condition of various leaf position cohorts over time is shown in Fig. 42. Note the overall poor condition of the shoots in June and December and the subsequent recovery in August and January. The June decline was caused primarily by *Neochetina* larvae, waterhyacinth mites, and *Acremonium* and the December decline was caused by *Neochetina*, *Acremonium*, and spider mites. Leaf production negated most of these effects within a month.

**Site 3: Everglades Conservation Area 3A**

The three sites studied within the Conservation Area were all quite different. Site A was located behind a levee and out of the main flow of the canals. As a result, the plants ultimately because sparsely distributed and developed large root systems with spindly leaf petioles. These are typical symptoms of a poor nutrient balance. Site B was located at the edge of the Miami Canal and, as a result, was always within a relatively strong current and received abundant nutrients. Site C was at the edge of a primary canal but was bounded on the canal side by an extensive stand of hydrilla and on the levee
Figure 42. Data showing average condition of waterhyacinth leaves of each leaf position cohort group over a time series. Condition is rated on a scale of 0% to 100% with 0% representing a completely dead leaf and 100% a leaf which is completely green and undamaged.
side by sawgrass and spatterdock. Because of these restraints on the flow characteristics of the canal, the water that flowed through this site was from the everglades grass flats to the north more than from the canal. Although the plants here did not become as spindly or sparse as these at site A, they were somewhat stunted and growth was not as luxuriant as those at site B.

Figs. 43 to 45 illustrate characteristics of the waterhyacinth populations at these sites which reflect differences among sites. Shoot densities were high in the spring at all three sites and decreased into the summer. The decrease at sites A and B was associated with an increase in plant size. As plant size decreased in the fall, density again increased. At site C, however, density remained low throughout the year and the low density did not seem to be related to plant size.

Although biomass data were only obtained from June through January, some very interesting comparisons were possible. Site A data seemed very erratic increasing dramatically in August then decreasing in September only to increase again in November, etc. This was, in fact, related to the heterogeneous nature of the site and sparse occurrence of the shoots resulting in a rather clumped biomass distribution. The coefficient of variation for site A increased from ca. 40% in July to nearly 90% in October after which it decreased to less than 20% in November.

Standing crop at site B increased steadily through late December. Variability was high in June and July with coefficients of variation at 115% but in September this value declined to less than 30%. This seems to be a typical pattern that one would expect as a newly developing mat forms where the population is relatively spotty early in the colonizing stage but increases steadily and becomes more evenly distributed as the colony becomes well established.
Figure 43. The average standing crop of the waterhyacinth populations in Everglades Conservation Area 3 at the three study sites (A, B, and C). The data represent grams dry weight per square meter.

Figure 44. Shoot density at the three study areas in Conservation Area 3 over the period of sampling from Mar. 1979 through Jan. 1980.
Figure 45. Data for canopy height as measured by the length of third position cohort leaves at the three study sites in Everglades Conservation Area 3 showing differing seasonal trends.

Figure 46. The percentage of the shoots found to be injured by *S. albipalpis* larvae at the three study sites in Everglades Conservation Area 3. The data show similar trends for sites 3A and 3C but a quite different seasonal pattern for site 3B.
Standing crop was least variable at site C. Coefficients of variation were highest in July at 40% and declined to very low values of ca. 3% by January. This probably exemplifies a stable, well established population in a confined situation with a limited growth potential. Curiously, though, this site attained the highest standing crop value of ca. 550 g/sq. m. in early September.

Counts of *S. albiguttalis* larvae indicated that they were both spatially and temporally erratic. Generally, more larvae were found at site B than A or C and counts were highest in the fall (Fig. 48). In December, however, larval counts were highest at site C. Very few larvae were ever found at site A.

Counts of pupae revealed a pattern similar to that of larvae. Counts were consistently highest at site B and generally extremely low at site A. Curiously, the highest counts were found in June and declined through the summer in marked contrast to larval counts. At site B peak pupal counts seemed to occur in a cyclical pattern approximating a 60 day period (Fig. 47).

The percentages of the shoots damaged by *S. albiguttalis* larvae at each of the three sites are illustrated in Fig. 46. Shoot injury was high at all sites in the spring and in the late fall to early winter. This declined to very low values during the summer at sites A and C. At site B, however, injury values remained high throughout the year. The exception was in late July but this was due to the diluting effect of a previously undamaged mat which had drifted in and mixed with the plants at the site. In general, *S. albiguttalis* populations were most intense at sites B, C, and A, in that respective order.

In summary, these represent parallel studies at three sites with differing water flow characteristics. At the time the studies were begun, the waterhyacinth plants were similar at all sites. Decreased water levels resulting from water management activities caused the plants at sites A and C to
Figure 47. A comparison of seasonal abundance of *S. albiguttalis* pupae at the three sites in Everglades Conservation Area 3

Figure 48. Same as Fig. 47 but data represent the average number of *S. albiguttalis* larvae
change towards a more spindly, erect form whereas the plant at site B retained the luxuriant, robust growth form. This was largely due to the increased influence of sheet flow of low nutrient water from the grass flats on the former two sites whereas site B was influenced by the high nutrient channelized flow of water through the canal. In the fall increased water levels enabled the plants at site C to recover but, possibly because of more stagnant conditions at site A, the plants there were not able to recover.

Infestations of *S. albiguttalis* were clearly influenced by the types of plants present within the sites. If one were to examine the data from only site A or C, one would suspect that *S. albiguttalis* infestations are very seasonal in nature. Site B shows this not to be true but rather that *S. albiguttalis* may be present in relatively high numbers throughout the year provided the proper plant type is present. This, in turn, depends on nutrient availability and flow characteristics of the site.

One difficulty experienced in these studies was the result of plants further upstream drifting into the sites or the plants at the site drifting downstream. As a result, entirely different populations could have been sampled from one time to the next. Study sites are not easily maintained in these free floating situations and impounding the plants may cause very different patterns of growth and cause a change in the shoot morphotype. We realized then that it was desirable to identify the same population of plants over subsequent time intervals and even possibly to identify individual shoots. Hence, we began testing methods of tagging individual shoots in order to track the fate of the plants over time and thereby assess the impact of biological control.

**Site 4: Lake Alice**

Studies were conducted at this site because a great deal of background data
were available and because this constituted one of the sites at which *S. albiguttalis* was released. In fact, the number of insects released here represented the largest quantity of this species ever released. During the spring of 1979 a total of 35,948 eggs, 17,145 larvae, 31 pupae, and 120 male and 85 female adults were released within a 75 m² area. Releases were continued on a monthly basis from February through May 1980 during which time an additional 19,682 eggs and neonates and 44 male and 38 female adults were placed within the same area.

By April 6, 1979, after the first releases, significant amounts of injury to the plants were apparent within the release area. In fact, aerial photos revealed a rectangular area of brown plants within the otherwise green waterhyacinth mat and this rectangle conformed with the boundaries of the release area as delineated by conspicuous corner posts. At this time, larvae were only found within the immediate release area. By 17 May damage was still evident but only one fifth instar larva was found and the infestation did not seem to be expanding. In June, although damage was still apparent, no larvae or pupae were found.

The same pattern was evident following the 1980 releases. In short, insects and damage could be found in the immediate release area within a short period of time following the last release. However, after the insects completed the first generation they seemed to disappear from the area. After the first releases it became doubtful that a population of *S. albiguttalis* had established itself at this site. However, in August 1979 a single male adult was found near an opening in the waterhyacinth mat which was bordered by a few small plants and was located ca. 250 m east of the release area. The only other evidence for establishment was the sighting of one female in July 1980 which was not captured and its identification therefore not confirmed. Subsequent to this, in July
1981, two adult males were seen and one was collected and used as a voucher specimen. Hence, it became apparent that a population had persisted in the area for over a year. We concluded that a population was established in the area but that it was a very marginal one.

The pattern of plant growth, particularly changes in canopy height, may have been an important factor in the failure of *S. albiguttalis* at this site. Figure 49 shows average plant height as measured from the longest leaf over the course of these two years. Between April and May of both 1979 and 1980 the canopy height increased rapidly. This was also the times when *S. albiguttalis* seemed to disappear. Observations at other sites indicated that *S. albiguttalis* seemed to prefer small plants with the robust or "inflated" type of leaf petiole and, after May, this type of plant was uncommon at Lake Alice. Hence, it may be that the proper form of plant is not present at this site for a sufficient period of time to enable *S. albiguttalis* populations to increase to damaging levels.

Obviously, because *S. albiguttalis* was so rare here, it never became an important control agent and the sampling procedure barely even detected it. Two plants were collected in samples in April 1980 which had apparently been injured by *S. albiguttalis* larval feeding and these plants were several meters from the release area. Otherwise no indication of *S. albiguttalis* induced injury was ever found in the samples. Nonetheless, a great deal of interesting data was collected.

Canopy height ranged from 10-15 cm in the spring to 65-70 cm in the summer. The smallest plants were found in March after the old tall leaves which had been injured by frost had died and as the shoots began to produce new leaves in a relatively open canopy. The taller plants began to appear as offshoot production increased the shoot density (Fig. 49) and petiole length increased in
Figure 49. Canopy height, standing crop, and shoot density at Lake Alice (site 4) from June 1979 to Dec. 1980. Canopy height is represented both as the average length of the largest leaves (solid lines) and as the length of the third cohort position leaves (dashed lines). Vertical bars represent one standard deviation on the leaf length data and one standard error on standing crop and density data.
response to crowding. Density peaked in April of both years at about 100 shoots/m² at which time variability also peaked and numbers as high as 240 shoots/m² were counted. Density seemed to decrease somewhat during the summer as the shoots became larger and competition for space intensified.

Standing crop (the dry weight of the total harvestable living plant material) values for 1979 and 1980 are also illustrated in Fig. 49. The two years were very dissimilar with a gradual increase through the summer of 1979 and a peak in October of ca. 1650/m² as contrasted to the more exponential increase in May through July of 1980 and a peak in July of ca. 1500 g/m². Hence, the peak was attained much sooner the second year after which standing crop values decreased slightly then seemed to remain more or less stable.

Leaf production data (Fig. 50) revealed that the plants grew extremely rapidly at this site. During the period of active growth (March to October) the shoots produced new leaves at an average rate of 0.126 per day or ca. 1 leaf every 8 days. During this period of time the average shoot bore ca. 5-7 live leaves so a complete leaf replacement occurred approximately every 40-50 days. Curiously, leaf production did not increase as the number of live leaves increased but rather remained relatively linear. Leaf production began to slow in October and November then practically ceased from December through February.

Leaf death lagged behind leaf production and occurred at a somewhat slower rate (one leaf died ca. every 10.2 days) so the number of live leaves per shoot slowly increased over the growing season from one to up to eight leaves per shoot. Leaf death rates seemed to remain constant even when leaf production slowed which resulted in fewer leaves per shoot in the winter.

Leaf production, turnover, and death rates may be very important factors to consider in biological control. If the replacement time for a leaf is
Figure 50. A leaf budget for tagged shoots at Lake Alice (site 4). The solid dots and line represent the cumulative total number of leaves produced by an average shoot over time. The dashed line and triangles represent the cumulative total number of leaves over time which had died. The open dots and solid line represent the balance between the two or the average number of living leaves per shoot on a given date. Note that during the growing season (Mar. to Oct.) leaf production (0.126 leaves per day) exceeded leaf death (0.098 leaves per day) and the number of leaves per shoot tended to increase.
less than the time required for a biological control agent to injure that leaf, then the importance of the biological control agent is minimal, no matter what the apparent injury appears to be. This would be especially true for those organisms which require a long time to develop and remain on a single leaf. In a case like this, the organism would appear to be restricted to the old leaves of plants which produce leaves rapidly whereas they may appear to "move-up" into the young leaves when or where leaf production is reduced. The spatial distribution of various organisms was studied at this site with this possibility in mind.

Leaf injury caused by certain species, such as the larvae of *N. eichhornia*, occurred much more frequently in the old leaves. Figure 51 shows the frequency of weevil larval injury on various leaf position cohorts over time. Periodically, frequency of injury to young leaves increased but generally this type of injury was most apparent in older leaves. Although injury to the younger leaves did seem to increase somewhat as leaf production slowed, injury to the youngest leaves (position 1-3) was rare.

Leaf injury caused by other species, such as the waterhyacinth mite and the zonal leaf spot pathogen (Figs. 52 and 53), became abundant only when leaf production rates began to decline. These peaked generally in the fall and early winter and, like weevil larvae, rarely caused injury to the youngest leaves. With both of these organisms there was a definite tendency to appear first in the older leaves and later in somewhat younger leaves. Also, there was a distinct tendency for these two organisms to occur together.

Species such as the spider mite seemed to appear in waves throughout the year. Spider mite damage to leaves generally peaked in frequency in the spring and in the fall (Fig. 54). The duration of occurrence of this damage was brief,
Figure 5.1. The pattern of Neochetina spp. larval injury to various leaf position cohorts over time (June 1979 through Dec. 1980). As noted at site 1, frequency of larval injury to young leaves tends to be low.
Figure 52. The frequency of leaf injury caused by waterhyacinth mites to various leaf cohorts over an 18 month period. Note that this organism was restricted to old leaves and generally only occurred in the fall.
Figure 53. The intra-shoot spatial distribution of leaf injury as represented by the frequency of leaf position cohorts with symptoms of zonate leaf spot infection.
Figure 54. The intra-shoot spatial distribution of spider mite injury to waterhyacinth leaves. Note that when these organisms appear they seem to infest all leaf cohorts but they vary seasonally.
generally decreasing to very low amounts during the summer and winter. Damage frequencies increased rapidly after the first occurrences were noted and no intra-shoot spatial patterns were apparent.

Leaf injury by larvae of the moth *Arzama densa* was almost always rare. Fig. 55 shows a tendency for damage frequencies to occur in a diagonal pattern. This results from the persistence of injury over the life cycle of the leaf, thus giving the appearance of the damage moving downward on the shoot. *Arzama* induced injury seemed to occur only in the summer and fall and to virtually disappear in the winter and spring.

Because the data represent frequency of occurrence of various types of leaf injury it is of limited usefulness where the important facet is quantity of injury. For example, adult weevils are nearly always present and almost all leaves bear signs of their feeding activity. Hence, if frequencies were calculated they would all be nearly 100%. For this reason, only the number of adult *N. eichhorniae* found on a per plant basis has been plotted (Fig. 56). Note the tendency for the weevil population to increase through the summer, to peak in the fall, and to decline prior to the onset of winter.

Other factors, such as frost, were not age specific and were always absent except for brief periods of time, in this case, during the winter. Injury caused by winter frosts tended to kill the older leaves and especially the taller leaves. This was the single most important factor in the rapid reduction of biomass. After the period of cold weather ended in the spring the plants quickly rebounded and recovered. Leaf production was nil until then so the shoots could not replace the leaves killed.

Trends in leaf condition are shown in Fig. 57. The contour lines represent lines of equal condition. As can be seen, the ultimate effect of all of
Figure 55. The frequency of leaf injury caused by the pickerelweed borer (*A. densa*) to leaf position cohort groups over time. Note that injury caused by larvae of these species was generally rare.
Figure 56. The relative population sizes of Neochetina eichhorniae adults at site 4 during 1979 and 1980. Numbers represent averages per 100 shoots examined. Vertical bars represent one standard error on either side of the mean.
Figure 57. The relative condition of waterhyacinth leaves of different leaf position cohorts over a 12 month period from June 1979 through May 1980. Average leaf condition is adjusted for relative abundance of a leaf cohort. For example, if average condition of leaves of a specific cohort is 80% but only 20% of the shoots possess leaves of that cohort, then the adjusted leaf condition would be 80% X 20% or 16%. Isoleths representing leaves of equal condition are indicated which show the change in position of leaves of equal quality over time.
these leaf mortality factors was to cause a decline of leaf condition in the fall which was accentuated when leaf production slowed and freeze damage became prevalent. The presence of few inhibiting factors and the rapid production of leaves in the spring resulted in a return of a healthy leaf complement within a very short time. Leaf condition peaked in August at a time when most factors apt to cause injury to the leaves had been low for two or three months.

Although studies at this site ultimately had nothing to do with the objective of evaluating the efficacy of *S. albiguttalis*, they were valuable in terms of developing a methodology for such evaluations. It began to become apparent that for these studies simple injury frequencies were not sufficient but rather some weighting for extent of injury was necessary.

**Site 5: Lake Manatee**

Studies were begun at Lake Manatee at a time when it appeared that Site 1 could be lost and it was desirable to retain a site in the west-central area of the state. However, continual interference from weed control practices resulted in the necessity of dropping the site after collecting data there only once. It is significant to note, however, that casual observations made through the summer revealed that *S. albiguttalis* infestations remained at damaging levels from May to September 1979. Data were collected at two sites on 21 June 1979 which enabled some interesting comparisons. Site A was on the east side of the lake in Gilley Creek while site B was on the southwest side within the state park. Plants at site A were ca. 65 cm in height with 27 cm roots and were not as robust as those at site B. Plants at site B averaged 52 cm in height with roots ca. 26 cm in length. *Sameodes albiguttalis* populations were high at site B but were very low by comparison at site A. *Neochetina eichhorniae* populations were about the same at both sites with averages of 140 and 127 adults and 47 and 40
larvae per 100 shoots for sites A and B, respectively. Interestingly, however, weevil larval damage was localized higher in the shoots at site A with more larval damage to younger leaves (Fig. 58).

*Acremonium zonatum* was present on 23 and 17% of the shoots and *Orthogalumna terebrantis* was present on 90 and 47% at A and B, respectively. Mites were more prevalent over all leaf cohorts at A whereas zonal leaf spot seemed to be more prevalent only on the older leaves (Fig. 59).

Spider mites and *A. densa* were generally unimportant with small percentages of the plants affected at both sites. Both did, however, seem to be predominant at site A.

*Sameodes albicyttalis* infested 50% of the shoots at site B and none at site A. Shoot injury was localized in the younger leaves with apical damage to almost all of the damaged shoots. This apical damage is apparent by the high frequency of injury to first cohort position leaves in Fig. 60.

In summary, *S. albicyttalis* and *N. eichhorniae* seemed to impact shoots at site B more than those at site A. The reverse was true for *A. zonatum*, *O. terebrantis*, *A. densa*, and *T. urticae*. As a result, leaf condition ratings were consistently lower at site B over all leaf cohorts (Fig. 61). Hence, we would conclude that leaf longevity is reduced more by *Neochetina* and *Sameodes* than by other factors.
Figure 58. A comparison of the intra-shoot spatial distribution of larval *Neochetina* spp. induced leaf injury at two sites on Lake Manatee.
Figure 59. A comparison of the intra-shoot spatial distribution of waterhyacinth mite and zonal leaf spot induced leaf injury at two sites on Lake Manatee.
Figure 60. A comparison of leaf condition among leaf position cohorts and the intra-shoot spatial distribution of larval S. albiguttalus induced leaf injury at two sites on Lake Manatee.
Site 6: Occidental Chemical Corporation

This site was chosen because during the surveys conducted to study the dispersal of *S. albiguttalis* a heavy infestation was found here. Three sites were established within the quarry. The first two, designated 6A and 6B, were studied concurrently beginning in August 1980 and continuing through January 1981 for site 6A and through April 1981 for site 6B. Plants at site 6A died out in January when the water level receded and several severe frosts occurred. Site 6B survived the winter by virtue of the fact that the water there was deeper and the plants thereby less exposed to extremely cold temperatures. Of the 10 tagged shoots at site 6B, four survived and six died between February and March. By April the plants had recovered but were small, the water level was up, and the mats were very mobile. As a result, the mat which contained the tagged shoots had drifted away from the site. After an extended search only one shoot was found (ca. 1 km distant) and site 6B was abandoned.

The two particular areas designated site 6A and site 6B were originally thought to be ideal sites for *S. albiguttalis*. Site 6A was heavily infested in June 1980 and, at that time, the plants were lush and healthy in appearance with large, dark green, soft leaves and *S. albiguttalis* was abundant. By the time the study was established in August, however, the plant morphotype had changed, possibly due to the low water level, to tall, spindly shoots with pale green, hard leaves, and the *S. albiguttalis* infestation had declined. Therefore, site 6B was also selected because the plants in that area appeared similar to the type originally present in site 6A and it was anticipated that *S. albiguttalis* populations would build up at site 6B in a similar fashion. However, possibly because it was too late in the year, populations of *S. albiguttalis* comparable
to those present at site 6A in June were never seen at site 6B during the period that data were collected.

The third site (6C) was established in May 1981. The "on-off" cycle of infestation at sites 6A and 6B was recognized as a problem and observations in the vicinity of site 6C during 1980 indicated that a *S. albiguttalis* population had persisted there for over a year. Hence, this site was selected based on the probability of the continued persistence of an *S. albiguttalis* population. It is important to note, however, that when this area was originally examined in August 1980 the waterhyacinth population was comprised of only a fringe of small plants along the shoreline. This fringe persisted until April 1981 when the plants drifted into other areas. In May a mat of small shoots with inflated leaf petioles and a light infestation of *S. albiguttalis* drifted into the area but the site was no longer typified by a fringe of plants, having instead a more or less solid mat.

Data for shoot density and canopy height for all three sites are illustrated in Figs. 61 and 62. Density of shoots was greater at site 6A than at 6B but the reverse was true of plant size as indicated by leaf length. Both density (of live shoots) and canopy height declined sharply in January in response to freezing temperatures. Again, it is apparent that the plants at 6A did not recover but those at 6B did. Site 6C seemed to be similar to site 6A in terms of the decline in canopy height that occurred in the fall. Note that at site 6B this pronounced decline was not present. As described earlier, these declining shoots became spindly with very hard, pale green leaves. Density at site 6C was quite high when the plants were small but decreased as size increased. Interestingly, in the fall shoot density underwent a concomitant decline with canopy height which is atypical of a healthy waterhyacinth popula-
Figure 61. A comparison of canopy height as estimated from third position leaf cohorts among the three sites at the Occidental Chemical Corp. quarry (site 6). Data for sites 6A and B are for years 1980-81 while those for site 6C are for 1981 only.
Figure 62. A comparison of shoot density at the three study areas within site 6
tion. Although it is normal for plants to become smaller in the fall this is usually accompanied by a responsive increase in density.

Leaf budgets for the three sites are shown in Figs. 63 and 64. At site 6A the shoots originally averaged ca. 7 live leaves each in August 1980. Continued growth produced an additional 5 leaves by October but almost 7 of the original leaves died in the interim. Hence, the number of live leaves per shoot declined. This pattern continued as leaf production slowed in November and December but leaf death continued resulting in a steady decline in the number of live leaves. Note the similar pattern at site 6C where it was apparent beginning in July that a decline was in progress. This should be contrasted to site 6B where leaf production was nearly able to compensate leaf death and maintain a full leaf complement until the sudden onset of frosts caused a rapid increase in leaf death. This site was apparently not in a state of decline.

A summary of the important factors which affected leaf condition at the three sites is presented in Figs. 65-67. Leaf condition weighted for relative frequency of occurrence is rated for each leaf position cohort and the extent of damage caused to each cohort by the most important mortality factors is indicated. The small arrow with a circled number indicates the hypothetical "same leaf" over time. Unfortunately, mortality factors were not rated for intensity until November 1980. Data before then only represented frequency based on positive or negative indications of injury and are not included in the figures. In August, however, none of the factors were nigh. Weevil larvae were present in leaves as young as the fourth cohort at 6A but were common only in sixth cohort and older leaves. Interestingly, by November, the frequency data indicated that Neochetina spp. larvae were in third position cohorts leaves but the data on intensity indicate that they did no significant harm to the leaves until the
Figure 63. A leaf budget for waterhyacinth plants based on averages per shoot at the Occidental Chemical Corp. site 6A. Leaf production represents the cumulative number of leaves produced over time beginning with the number of live leaves per shoot on the day the plants were first tagged. Leaf death represents the cumulative number of leaves dying over time not including dead leaves initially on the plant. Live leaves represent the number of living leaves per shoot on each date and should be the balance between leaf production and leaf deaths.
Figure 64. The same as Fig. 63 except data are for site 6B (Aug. 1980 - April 1981) and site 6C (May - Nov. 1981)
Figure 65. Leaf survivorship curves and mortality data for leaf position cohorts of waterhyacinth shoots at site 6A. The leaf condition or survivorship data represent the average condition (scaled from 0 to 100) multiplied by the relative frequency of occurrence per cohort (scaled from 0 to 1). The height of the bars represents total mortality within that cohort considering only the major factors. The portion of each bar attributable to a given mortality factor is proportional to the contribution of the factor to total mortality. The small arrows with attached circled numbers simulate a tagged leaf which changes position and condition over time (the same number represents the same leaf).
Figure 66. Same as Figure 65 but data for site 6B. See Figure 65 for legend.
Figure 67. Same as Figure 65 but data for site 6C
sixth cohort (Fig. 65). In December and January weevil larval damage was still confined mainly to the older leaves at site 6A.

At site 6B weevil larvae were present in third position leaves in August but were not common until the seventh position and older cohorts where more than 50% were infested. In September larval damage was still not found in any leaves younger than third position and again did not exceed 50% until seventh position and beyond. By November the trend remained about the same but over 70% of seventh position and older cohorts were infested. Damage severity was low, however, increasing to significant levels only within sixth position cohorts and older (Fig. 66). In December the distribution and intensity of weevil larval injury changed very little but by January damage to third position cohorts became ubiquitous with the damage relatively severe to fifth position and older leaf cohorts. By March, when the shoots were recovering from the winter, weevil larval damage had become rare but by April it was present again in third position leaves. If one examines the leaf production data, it becomes apparent that weevil larval damage did not "appear" to move up into the youngest leaves until leaf production had ceased or, at least, had begun to slow down. Thus, leaves of the various cohort groups would be older than those of the same groups present when the plant was actively growing.

The distribution and intensity of leaf damage caused by Neochetina spp. larvae were quite different at site 6C and it is unclear whether this represents site or seasonal differences. Larval damage was present in all leaf cohorts including the first position in May (Fig. 67). Active growth produced an average of over five new leaves by mid-June and this "appeared" to push the larval damage back to the seventh cohort position and damage was not severe. By July damage was present in third position leaves but was not severe except on
seventh position and older leaf cohorts. By August it had advanced to first position leaves and was beginning to become severe in leaves as young as second position cohorts. Weevil larval damage remained prevalent in the young leaves through the remainder of the year.

Only three other factors were important to leaf mortality at this site. These were weevil adults, frost injury, and undefined browning of the leaves that did not appear to be pathogen related. Weevil adult feeding was ubiquitous and relatively constant although it did become somewhat more severe in the fall. Frost injury was prevalent in all leaf position cohorts but only in December and January.

The leaf injury described as "browning" appeared to be related to plant nutrition and size. As the plants began to decline they first turned pale green and later, brown. At site 6A this browning first appeared on seventh and eighth position leaves in August, then progressed to third position leaves by October and to first position leaves by November although it remained most severe on older leaves. The older leaves, being taller than the newer ones, were retained upright in the mat and as they browned were more apparent than if they had been in the lower canopy. As a result, the entire mat acquired a dark brown coloration. The same pattern was true for site 6B although it was less severe (Fig. 66) and remained more in the lower canopy. At site 6C the browning was present on old leaves in May and progressively moved to the younger leaves until September when it was present on the youngest leaves (Fig. 67). We have no explanation for exactly what caused this brown leaf condition.

The effects of these various mortality factors on leaf survivorship are apparent in Figs. 65-67. As the various factors increased in frequency and intensity, leaf condition declined and this decline was usually evident on the
older leaves first. As the effects accumulated and leaf production slowed, the condition of the younger leaves deteriorated. As a result, the overall condition of the shoots was decidedly worse in the fall than in the spring or summer.

A summary of this site is presented in Figure 68 using only first position cohort leaves for 6A and 6B data combined. This basically shows that, except for frost, no identifiable mortality factors other than the waterhyacinth weevils had a significant impact on these leaves. In 1980 weevil populations were low and first position leaves were normally in nearly perfect condition. In 1981 weevil populations increased and leaf condition decreased.

Unfortunately, the data gathered at this site failed to show any impact by *S. albiguttalis* at this site. This is in spite of the fact that in June 1980, the size of the *S. albiguttalis* population in this area was the largest we had ever seen anywhere and damage to the plants was extensive. In July 1981 a heavy infestation was again found at site 6B after we were no longer collecting data there. Hence, *S. albiguttalis* may yet be an important control agent but a sporadic, unpredictable one.

**Site 7: Everglades Conservation Area 2A**

This study was begun on 24 October 1980 at which time 15 waterhyacinth shoots which were free of *S. albiguttalis* infestation were selected, tagged, and replaced in the waterhyacinth mat along the edge of a canal. The evaluation procedure followed was as described in procedure 5. At the time of the initial tagging *S. albiguttalis* injury to the plant population was so extensive that it was difficult to locate unaffected shoots for the study. For the first follow-up observation the plants were re-examined on 4 November at which time the site was found to have been treated with a herbicide and only 2 of the tagged shoots
Figure 68. Data for first position cohort leaves (youngest leaves) from sites 6A and 6B showing the effects of frosts on leaf condition in January and February 1981 and the buildup and effects of waterhyacinth weevil larvae and adults in the summer of 1981.
were recovered. Therefore, the data taken at this site are of little value when considered alone. However, it does provide some insight into existing conditions at an extensively managed site. Evaluations were based on leaf conditions ranging from 0 to 100 and injury frequencies weighted from 1 to 4.

When the shoots were first tagged the number of living leaves averaged ca. 6 per shoot, the shoots were small with the inflated type leaf petioles, and shoot density was ca. 150 per sq. m. The only significant factors affecting living leaves were weevil adults and spider mites. Weevil adult injury was not extensive with only ca. 25-30% of the leaf area affected. Spider mite injury was low on the younger leaves but involved up to 40% of the leaf area on cohorts 3 to 5. Waterhyacinth mites were moderate on cohorts 5 and 6 and zonal leaf spot was moderate to heavy on cohort 6 leaves with ca. 45% of the leaf area involved. A total of 75% of the 16 shoots had at least 6 leaves whereas only 25% had 7 leaves indicating that leaf number was very constant.

When the site was re-examined in November, the two shoots found each had eight live leaves. Adult weevil injury was still light but was present on all leaves. Waterhyacinth mite damage was less than before and zonate leaf spots were only on cohort 6 and older leaves. Spider mite injury was present on cohort 5 and older leaves but was extremely light. Interestingly plant density increased dramatically from 150 to 256 shoots per sq. m. Overall, plant injury caused by insects, mites, or pathogens was very scant, indeed. This raises some interesting questions. Does the need to engage in extensive waterhyacinth management efforts arise from the lack of biocontrol agents, or...does the lack of biocontrol agents arise from extensive herbicide use?

Site 8: Snake Creek

This also represents a site where most of the tagged shoots were lost and
minimal data were obtained. After the first follow-up examination the site was dropped and further studies were moved to DeLand on the St. Johns River (Site 10).

The first group of 15 shoots was tagged on 30 October 1980. The third position leaves on these shoots averaged 24 cm in length. Plants damaged by *S. albiguttalis* were present but only shoots without damage were selected for tagging. Plant density averaged 65 shoots per square meter and the average number of live leaves per shoot was 6.1. The effects of various mortality factors were evaluated using Procedure 5 as described in the Methods and Materials Section.

The average condition of the youngest two leaves was 100%. Between cohorts 5 and 7, average condition dropped from 96% to 69% and at position 9 it was only 5%. Leaf condition averaged over cohorts was 75%. The factors causing the most injury to the first 5 leaf cohorts were *Neochetina* spp. adults and spider mites. *Senescence* and *Acremonium* caused injury to cohort 8 and older leaves. Only 8% of all leaves were damaged by *Neochetina* spp. larvae and the average proportion damaged on affected leaves was less than 25%. *Neochetina* spp. adult feeding injury occurred on 64% of all leaves, but the average proportion damaged was less than 25% on more than half (57%) of the affected leaves. The remaining 7% of the affected leaves had average injury ratings of 26-50%. *A. zonatum* damaged 53% of all leaves but the proportional injury ratings per leaf were less than 25% on 41% of the leaves and between 76 and 100% on 9% of the leaves. Spider mites damaged 25% of the leaves and 19% were damaged by waterhyacinth mites. Most of the mortality factors affecting leaf condition were rated at less than 25%. The exceptions were senescence and pathogens which affected only oldest leaves.

On 10 Dec 1980, the waterhyacinth mats had shifted and the plants had
floated out into the river. The tagged shoots and the red flags used to mark their locations had been moved. Some of the flags were stuck into the mud along the banks of the creek, probably by fishermen. Many of the waterhyacinth shoots in the tagging area had been fed upon by cattle. Three of the tagged shoots were located several hundred feet from their original locations and \textit{S. albifluttalis} larvae had damaged three leaves on one shoot. The procedure was changed slightly at this time and mortality factors and leaf condition were then rated from 0-100. Each of the three tagged shoots had produced 5 new leaves and had an average of 5 live leaves. Most of the leaf damage was caused by cattle browsing on the shoots and, as a result, ca. 54% of the leaves were partially missing. The average leaf condition for cohort 1 leaves was 89% whereas it was 100 at the previous observation. Average condition for cohort 5 decreased from 96 to 56 and was 0 for positions 10 and 11. Leaf condition averaged over all cohorts was 42%. \textit{Neochetina} larval damage increased to 35%, most of which was rated 10-20% with 7.7% of the leaves having 30% damage. Spider mite damage was rated less than 25 on 15.4% of the leaves. The number of shoots damaged by \textit{Neochetina} adult feeding decreased from 87% in November to 67% in December. Spider mites damaged 67% of the shoots in both October and December. Average length of the third leaf declined slightly to 21 cm in December.

\textbf{Site 9: Lake Okeechobee}

The first study site established in Lake Okeechobee was located in Fisheating Bay south of a line of spoil islands. The waterhyacinth mat occupied an area of ca. 3700 sq. m. and was intermixed with water lotus (\textit{Nelumbo lutea}). Most of the waterhyacinth shoots in this area qualified as the type of plants ordinarily infested by \textit{S. albifluttalis} based upon the criteria of color, shoot size, and petiole shape. The waterhyacinth occurred in small, scattered clumps
throughout the study area which was on the lakeward edge of the emergent littered zone. The shoots within the clumps ranged in size from 6 to 40 cm with the taller shoots in the center and the shorter shoots at the periphery. Although signs of *S. albiguttalis* were present in the area, the shoots which were tagged were deliberately selected as not having been injured by *S. albiguttalis*.

Data were collected three times in this area beginning on 6 Nov. 1980 and through 5 Feb. 1981. Mean shoot size changed little remaining between 10-15 cm. Plant density changed drastically, however, as a relatively large, crescent shaped mat developed and became relatively continuous along the eastern edge of the *Nelumbo* area. Between December and February shoot density increased from 84 to 204 per sq. m. Leaf production was relatively slow, averaging only 0.085 leaves per day which would require ca. 12 days for the production of one leaf per shoot. Leaf death exceeded leaf production over the 81 day period resulting in a decline in the number of live leaves per shoot from 8.8 to 4.5. A total of ca. 10.5 leaves died per shoot as compared to ca. 7 produced.

Data showing the leaf mortality factors affecting the tagged shoots in this area are illustrated in Fig. 69. In May the shoots bore many leaves and the first eight were in very good condition. The only factor affecting the younger leaves was adult weevil injury. Weevil larvae were present beginning with fourth position leaves but caused very little significant injury on any of the cohorts.

By December several factors had increased in intensity on the older leaves, most of which was comprised of weevil larvae and zonate leaf spot injury with the undefined browning of the leaves that was noted for site 6. Each shoot still bore an average of eight live leaves; however, the overall con-
Figure 69. The data for tagged plants at Lake Okeechobee site 9A showing the relative condition of the various leaf position cohorts and the factors responsible for affecting leaf condition. The small circled number represents the position of the same tagged leaf over the 81 day period.
Figure 70. The data from site 9B at Lake Okeechobee for tagged plants showing leaf cohort survivorship (line) and the factors which contribute to leaf mortality (bars). The small circled numbers indicate the position of the same leaf on subsequent dates.
dition of leaves 6 to 8 was not as good as that in November. The browning undoubtedly resulted from the older leaves remaining in the canopy longer as a result of the slowed leaf production and turnover. Also in December very small amounts of *S. albicuttalis* induced injury were present.

By February, winds had shifted the mats within the bay and only two of the tagged plants were recovered. Leaf condition had declined but the three or four youngest shoots were in good condition. Almost all leaves present in December (52 days earlier) were dead. *Sameodes albicuttalis* larval injury had increased in intensity and *A. densa* larval injury was apparent. Signs of frost injury were present on seventh position and older leaves and the general brown appearance was present on leaves as young as third position cohorts and was quite heavy at fifth position and beyond.

A second study site (9B) was established in April 1981 near King's Bar where waterhyacinth was growing amongst giant bullrush (*Scirpus californicus*). It was hoped that the bullrush would prevent the waterhyacinth from drifting out of the area. Again, the shoots at this site qualified according to the morphological characteristics that, in our opinion, distinguish the plant form that *S. albicuttalis* prefers. The size of the shoots remained relatively constant with the average length of third position leaves ranging from 15-18 cm during the 78 day period (29 April to 16 July). Shoots were selected for tagging at random and most showed symptoms of *S. albicuttalis* larval injury. Shoot density averaged 83 and 107 shoots per sq. m. in April and May, respectively.

Early in May, shortly after the shoots were tagged, drought began to affect the site. Water was so shallow in late May that it was possible to collect data on foot. Weather conditions prevented access to the site in June but by July the area had completely dried out and most of the tagged plants had desiccated.
Data showing plant condition and relative intensities of leaf mortality factors are presented in Figure 70. In April S. albicuttalis larvae were the single most important factor causing injury to the shoots in the study area. Even young leaves were affected and the overall condition of leaves in positions 1-4 was much lower than would otherwise be expected.

In May plant condition deteriorated further. Leaf production had been very slow over the past month with an average production of only 1.5 new leaves per shoot. Nearly seven leaves per shoot died on average resulting in a decrease in the number of live leaves from an average 7.3 in April to only 2.1 in May. S. albicuttalis damage increased in frequency and intensity and the youngest leaves were in very poor condition as a result. The decreased water levels caused early symptoms of desiccation on some leaves and the general browning described earlier was apparent on older leaves due to reduced turnover rates.

By May, the shoots were dead for all intents and purposes. Only three of the 13 shoots were found alive and these, ironically, were the only three not damaged by S. albicuttalis. Six shoots were killed directly by S. albicuttalis larval injury. It appears that if larval injury did not kill the shoots outright then they were much more susceptible to desiccation and the smaller shoots died first. On average, each shoot bore only 0.3 live leaves and had produced only 1.3 new leaves over the previous 50 day duration. In reality, however, the living shoots had produced 7, 6, and 4 new leaves or a respectable average of 0.113 leaves per day. Overall, the combined affects of S. albicuttalis and drought virtually eliminated the plants at this site and the study was discontinued.

In January 1982 a population of waterhyacinth was found in a moat-like
slough which surrounded King's Bar. The area was bordered lakeward by bullrush and by cattail near the island. Water within this slough was ca. 30 cm deep when a third study was initiated in this area on 18 January 1982. In this study the number of shoots sampled was increased. S. albiguttalis damage was estimated from all plants included in ten 0.25 m$^2$ samples. Plant morphometrics and the various leaf mortality factors were determined from four shoots subsampled from each of the ten 0.25 m$^2$ samples (40 shoots total). Leaf production data were based upon 30 tagged shoots and only the number of new leaves produced was taken on each observation date. A leaf budget was estimated by combining the 40 shoot data for number of live leaves per shoot with the leaf production data.

Unfortunately, in this latter study, the infestation levels of S. albiguttalis were not nearly as great as they were at this same site the previous summer. The total number of shoots injured by larval damage peaked at 4% in January and decreased thereafter (Fig. 71). Most of the damage noted was caused by early instars and was not seriously injurious to the shoots.

The data in Figures 72-74 show the change in plant morphology that began in April. Shoots increased in size from less than 10 cm to over 30 cm but root length increased proportionately less. The leaf laminae increased in size and length began to exceed width. This indicates that the stand was becoming dense and the leaf blades were transforming into a more erect, lanceolate form. Leaf petiole diameter decreased indicating that the petioles were becoming thinner and the diameter at the base began to approach, and later exceed, that at the mid-point indicating a change in form from the "inflated" type towards the "elongate" type. All of these characteristics indicate that the waterhyacinth mat was changing from a colonizing phase into an established population. In addition, density eventually decreased in response to increased competition.
Figure 71. The percentage of waterhyacinth shoots injured by S. albivittalis larval feeding during the first seven months of 1982 at site 9B in Lake Okeechobee as compared to the average shoot density at the site. Note that shoot density declined in the summer as shoot size (Fig. 72) increased.
Figure 72. Data for the average length per shoot of third position leaves and of the roots showing the changes in plant characteristics that took place over the course of the study at site 9B in Lake Okeechobee in 1982.

Figure 73. Same as Figure 72 but data for the average length and width of third position leaves.
Figure 74. Same as Figures 72 and 73 but data for the leaf petiole width at the mid-point of the petiole as compared to the width at the base.
amongst the larger shoots. The greatest changes occurred in July and these were concurrent with the end of the drought and the return of deep water (4+ m).

Very few factors were apparent which may have caused injury to the shoots during the seven month study period. Frost injury was extensive on almost all leaves in January but by February it was absent on the two youngest leaves and heavy only on fifth position cohorts and older. In March frost injury was no longer evident. *S. albiguttalis* larval injury was present January through April but average injury ratings never exceeded 2% for any leaf cohort. Injury caused by adult weevils was always present on all leaf position cohorts but injury ratings never exceeded 7%. Spider mite injury was light on leaf cohorts 3 through 7 in July and relatively heavy in August with ca. 10-20% leaf injury on average to seventh leaf position and younger cohorts. Waterhyacinth mites first appeared in April with only 1% leaf injury to positions 4 through 6. This increased to third position leaves by June and averaged 2 to 5% on positions 3 through 10 only to decrease again in August. Zonate leaf spots appeared in May and persisted through July but leaves were never heavily infested with generally less than 5% injury.

Weevil larvae were responsible for most of the leaf injury observed at the site and spatial and temporal trends are illustrated in Fig. 75. Weevil larval injury was noted in January but was light on young leaves and became somewhat heavier on older leaves. Damage increased in intensity and moved towards younger leaves through April, May, and June, then decreased somewhat in July only to increase again in August.

Data on leaf cohort survivorship are shown in Fig. 76. All leaf position cohorts were in relatively poor condition in January but this was due primarily to frost damage. The production of new leaves and the lack of recurrence of
Figure 75. A three-dimensional representation showing the spatial distribution of Neochetina spp. weevil larval injury to waterhyacinth shoots over time.
Figure 76. A three-dimensional representation showing the change in average survivorship of leaf position cohorts over time. The arrows and circled numbers represent the average change in the same leaves.
frost produced shoots with healthy young leaves but persistent frost damaged older leaves in February. In March and April young leaves remained in good condition and older leaves improved. This was a result of the oldest, frost injured leaves having been replaced by leaves which had not been subjected to frost injury. In May the condition of all but the very youngest leaves degraded. The only factor which was sufficiently intense to cause this was weevil larval injury. In June and July, as weevil larval injury decreased, leaf condition improved only to degrade again in August as weevil larval injury again increased. Hence, it appears that weevil larval and adult feeding were the only factors at this site which were sufficiently intense and persistent to influence the leaf dynamics of the plants. The effect was slight, however, owing to the fact that the plant population was new and the weevil population had not yet built up to damaging numbers.

Leaf budget data are presented in Fig. 77. Note that leaf production and leaf death are divergent resulting in a gradual increase in the number of leaves per shoot. This is typical of a thriving, growing population of waterhyacinth. The leaf production rate of 0.137 leaves per day is quite rapid. At this rate, each leaf destroyed would be replaced in approximately a week and the entire leaf complement of five to seven leaves could be replaced in 35 to 50 days.

In summary, the data at Lake Okeechobee from these three studies confirmed the unpredictability of S. albigutta. Data from the first study showed little effect of S. albigutta but, over the four month period, an infestation had begun in the plants that had been selected because they were initially uninfested. Unfortunately, the plants were lost before their ultimate fate could be determined. Data from the second study showed that S. albigutta would attack plants that were growing in wet soil or muck and that the combined effects of
Figure 77. Leaf budget data for waterhyacinth shoots at site 9B on Lake Okeechobee during January to July 1982. Leaf production is derived from 30 tagged shoots but live leaves per shoot data are based upon 40 randomly sampled shoots. Leaf death is calculated from live leaves present and new leaves produced (Dead = Original No. + New - Present No.).
larval injury and desiccation were lethal. This combined effect killed smaller plants first but eventually killed larger ones as well. Only uninfested shoots survived the drought although even these probably died after the study ended due to the long duration of dry conditions. The data from the third site are of interest because it shows the sequence of events that lead to the recovery of a waterhyacinth population following a catastrophic decline. In this case, the catastrophe was drought. This greatly reduced the waterhyacinth population and probably concentrated the insects on the few surviving shoots which further increased plant stress. The reduction of the plant population ultimately led to the reduction of the insect population. The plant populations increased quickly when the water levels increased but there was no simultaneous increase in insect populations due to the lack of refugia. As a result, the recovery of the plants was uninhibited and the shoots showed few signs of significant injury.

Site 10: St. Johns River

Data were collected on the St. Johns River at site 10 near DeLand from January through September 1981. The methods used were those described in Procedure 6 which involved repeated observations on the same waterhyacinth shoots over time. Shoots were identified by placing plastic tags on the youngest leaves on each observation date. However, shoots tagged in January were not recovered in February apparently due to drifting of the mats. Therefore, in March new shoots were tagged and floating PVC pipe frames which were tied to stakes were used to retain the shoots.

In January, frost injury was extensive on the leaves and the apical buds of several shoots had been frozen. Various S. albiguttalis larval instars were present but leaf injury was restricted primarily to older leaves. In February, the plants had recovered from the frost and frost injury was only apparent on

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leaf position cohorts five through seven. The plants were dark green and appeared luxuriant but *S. albiguttalis* larval damage was apparent on all leaf positions, although it was generally not severe.

Figure 78 shows the trend in the size and density of the shoots at the site during the study. Plant size decreased as they recovered from frost and density increased. This is caused by two factors. First, the larger "summer" leaves were killed by the frost and replaced by smaller leaves in the spring. Second, the shoots had begun producing ramets so many smaller shoots were present which tended to reduce mean values. Plant density and shoot height tended to be "mirror-images" of one another which reflected the trade-off that occurs between number and size.

The data on leaf survivorship and mortality are presented in Figure 79. The frost damage and its affect on survival of sequential leaves is clearly shown in the January data. In March, however, when new shoots were tagged, only *S. albiguttalis* larvae affected the younger leaves. By April, *S. albiguttalis* larval injury increased in severity and frequency, weevil larvae had substantially injured some of the older leaves, a conspicuous leaf mottling of unknown origin had become common, and the shoots were in generally poor shape. The trend continued in May and shoot condition degraded further but by June the plants had begun to outgrow the effects of the insects and had begun to recover. Each shoot had produced an average of ca. 4 new leaves between May and June and, as a result, were in much better condition. When the site was examined in July it was found that spray crews had treated 80% of the site with herbicide and most of the plants were dead. The few that remained were infested by *S. albiguttalis* and weevil larvae. Plants recovered quickly, however, and by August the surviving shoots had produced five new leaves, on average. Many new ramets were
Figure 78. Data for site 10 on the St. Johns River near DeLand showing annual variation in shoot size and density.
Figure 79. Data on leaf survivorship and mortality of tagged shoots in the waterhyacinth population at site 10 in the St. Johns River. The lines and circles represent the combined average leaf condition and relative frequency of occurrence for each leaf position cohort. The height of the bars represents the sum of the average damage ratings for all of the factors which cause injury to the leaves. The smaller sections of the bars represent the fractions of the total injury caused by individual mortality factors. The small circled numbers represent tagged leaves and show the change in position of the same leaves over time.
present and most bore four leaves. The apparently sharp decline in Fig. 79 in August for the fourth to the fifth leaf positions reflects the bimodal population of new ramets and older surviving shoots. This is largely a herbicide effect. Note that the young leaves again had very few factors affecting them whereas older leaves still bore symptoms of injury. In September the shoots were in very good condition, insect damage was mostly minor and on the older leaves, and *S. albiguttalis* larval injury was not apparent. This was apparently due to the reduction of insect population caused by the chemical removal of the plants, the subsequent rapid recovery of the plant population, and the slow recovery of the insect populations.

Figure 80 shows the leaf budget for the tagged plants. Over the term of the study each shoot produced an average of ca. 24 leaves or one leaf every 7.8 days (0.128 leaves per day). Although the trend was nearly linear, leaf production tended to be somewhat faster later in the year. Leaf death occurred at about the same rate as leaf production (0.127 leaves per day) and, as a result, leaf production compensated for leaf death and the number of live leaves per shoot was nearly the same in September as it was in March. Plants which had been killed by herbicide, however, were not included in this data because the number of leaves they had produced before they were killed was undeterminable. The rate of leaf production observed at this site was among the fastest and these high rates tend to displace injured leaves in a very short time.

Of the ten shoots originally tagged in March, all were recovered in April. In May four of the original ten were alive, two had been killed by *S. albigutta* *lalis*, two were lost, and three new shoots were tagged. In June four of the original ten were still alive but, of the three tagged in May, one was alive, one had been killed by weevil larvae, and one by *Arzama* larvae. Six new plants
Figure 80. A leaf budget for tagged shoots at site 10 showing the cumulative total number of leaves produced per shoot, the cumulative total number of dead leaves, and the average number of leaves alive on each shoot at each observation. Note that leaf production and leaf death were about equal resulting in no change in the number of leaves per shoot over the six month term of the study.
were tagged to bring the total present to 12. By July only one of the original ten shoots was alive, three of these as well as four tagged in June and one tagged in May were dead as a result of the herbicide treatment. One of the shoots tagged in June was also alive and two had been killed by *S. albiguttalis* larvae. No new shoots were tagged. The two living shoots were found again in August and eight new shoots were tagged. Most were lost by September but three remained, one original, one tagged in June, and one tagged in August. Of the 29 shoots tagged, three survived, seven were killed by *S. albiguttalis*, one by weevil larvae, seven by herbicide, and nine were lost. Of the shoots lost some may have been killed by insects but none were killed by herbicides since all plants were accounted for after they were treated. It may be stretching a point, but, over the six month period, as many plants died from *S. albiguttalis* injury as died from herbicide injury.

Of the ten plants tagged in March, five or 50% were killed by *S. albiguttalis* by the end of May. One was damaged but survived and this single plant demonstrated the ability of waterhyacinth to sustain a great deal of damage yet ultimately renew itself. In March, of the six leaves, those in positions two, three, and six were damaged by *S. albiguttalis*. By April the shoot had produced five new leaves, a total of seven were alive, and *S. albiguttalis* injury had increased and was apparent on positions four, seven, eight, nine, and eleven. That on position four and nine was new and the others were the same leaves from the previous month but the injury had increased even on those. By May the shoot had produced an additional four leaves, thus increasing the position of the leaves by four, and damage was only present on leaf positions 8, 11, and 12. These leaves were already damaged in April when they were in position 4, 7, and 8, respectively. By June an additional four leaves had been produced, the shoot bore
seven live leaves, and none of the leaves showed signs of *S. albiguttalis* injury. By this date *S. albiguttalis* had injured five leaves but the shoot had produced 13 in addition to the original six which were on the shoot in March. An additional 14 leaves had been produced by the shoot in September and *S. albiguttalis* injury to it was not observed during that time. It is instructive to note the change in size of the shoot that occurred over the duration of the study. In March the length of the third position leaf was only 9 cm. The new third position leaf present in April was also only 9 cm, but the one produced in May doubled to 18 cm. Thereafter it continually increased to 25, 39, 41, and 44 cm in June, July, August, and September, respectively. Based on this we would conclude that *S. albiguttalis* generally attacks shoots in their early growth and frequently kills them. If the injury is not fatal, however, the plant will outgrow the injury, *S. albiguttalis* will probably not re-infest when the plant becomes larger, and the shoot will survive. All shoots that died as a result of *S. albiguttalis* infestation were severely damaged on first position leaves which also usually involves damage to the stem apex and the terminal bud.

**Site II: Coral Springs**

The first site studied at Coral Springs was in an asphalt-lined pond which was one of a series of five such ponds being used by University of Florida scientists to study the ability of waterhyacinth to remove pollutants from sewage effluent. The ponds occupied a total area of ca. 200 sq m and the first pond to receive sewage effluent from the Coral Springs sewage treatment facility was twice the size of the others or about 67.5 sq m. Effluent was pumped into this pond at the western end and circulated anti-clockwise through the other ponds (see Fig. 20). Waterhyacinth in this pond were not harvested
while those in the others were harvested at one to two week intervals. A great deal of _S. albiguttalis_ activity was notable in the larger pond near the input so a series of tagged plants was placed in this area. The study was conducted from May to September 1981. At this time the plants in the study area were dark green, ca. 40 cm tall, and the density was ca. 100 shoots per sq m. Both density and size decreased through the summer which is indicative of a population decline. By September the shoots were generally 10 to 15 cm tall and the density was less than 30 shoots per sq m. This decline appeared to have been induced by the high _S. albiguttalis_ infestation.

Data for leaf cohort survivorship and mortality are shown in Fig. 81. As noted above, in May the leaves were generally in good condition and few factors were impacting the shoots. At this time _S. albiguttalis_ was moderately high but was the most important type of injury present. Weevil larval and adult damage were also present but not as extensively. By July weevil larvae and adults, _S. albiguttalis_ larvae, and even _Arzama_ larvae had combined to place a great deal of stress on the plants and the shoots were in very poor shape. An additional factor was present which was classified as unknown but was probably secondary bacterial rot associated with the heavy insect damage. This sort of secondary infection is very common on waterhyacinth in high nutrient sewage lagoon situations.

By August seven of 18 tagged shoots were killed by _S. albiguttalis_, two were dead from a stem rot, four were dead from unknown causes, three were lost, two were still alive, and seven new shoots were tagged. Living shoots were in very poor condition with _S. albiguttalis_ larval injury to young leaves, weevil larval damage to old leaves, and weevil adult feeding injury to all leaves. By September shoot condition deterioriated further with weevil larval
Figure 81. Leaf cohort survivorship (lines and circles) based upon combined relative frequency of occurrence and average condition of leaf cohorts and leaf mortality percentages (bars) based upon damage to leaves of various cohorts by specific mortality agents which partially injure or completely destroy waterhyacinth leaves. Legend as in Fig. 79.
Injury increasing in importance and *S. albiguttalis* injury decreasing. *Arzama densa* larval injury was prevalent in young leaves and the unknown factor was common on all leaf position cohorts. Of the two shoots which were still alive in August, one was lost and one had been killed by *S. albiguttalis*. Of the seven new shoots tagged in August four were alive in September, one had been killed by weevil larvae, one by *A. densa* larvae, and one by stem rot.

The leaf budget for site 11A is shown in Fig. 82. Note that as the percentage of shoots attacked by *S. albiguttalis* decreased, leaf production rates increased. The overall average rate of leaf production was 0.105 leaves per day but between 29 May and 6 July the rate was 0.04 leaves per day and during the last month it had attained a rate of 0.192 leaves/day. The rate of leaf loss remained more linear and averaged 0.124 leaves per day, hence, averaged over the 97 days, the shoots suffered net losses of live leaves. Plants at this site appeared to be on the verge of collapse in August but by September it seemed that they would recover since leaf production had begun to make significant gains. Unfortunately, we were told that the plants in the pond would be harvested and the study was terminated before the final fate of the shoots was known.

In October studies were begun in one of the earthen settling ponds located north of the asphalt ponds (see Fig. 20). The pond selected had a healthy fringe of waterhyacinth at that time and a relatively heavy *S. albiguttalis* population. On 13 October the average size of the shoots was ca. 20 cm and shoot density averaged ca. 160 per sq m. Shoot height was nearly the same on 27 October and 12 November but density increased dramatically to 310 shoots per sq m. Initially the leaf laminae were considerably wider than long (7.5 cm by 5.5 cm) but over the 30 day period laminae width decreased and length increased.
Figure 82. Leaf budget for tagged waterhyacinth shoots in a pond which received secondarily treated sewage effluent at the Coral Springs sewage treatment plant (site 11A). Note that the budget does not quite balance due to the fact that dead and lost shoots were replaced with live shoots. The bars reflect the percentage of the tagged shoots infested by *S. albiguttalis*.
(to 7.1 cm by 6.4 cm) as the lamina shape changed. The shape of the petioles also changed as the diameter at mid-point decreased (from 2.1 cm to 1.6 cm) while that at the base increased (from 1.0 to 1.2) indicating that the petioles had taken on a more linear and less swollen form. Hence, the shoots remained small but became harder in texture and more spindly in form. It is significant to note that this change occurred within two weeks (by 27 Oct.). Also at that time it was noted that the water level was low and the personnel responsible for maintaining the ponds were notified. They then increased the flow rate into the pond which subsequently raised the water level. In addition, of the plants sampled 100% were damaged by S. albugullalis. Hence, it appears that shallow water and a heavy S. albugullalis infestation caused the change in plant form.

On the map of the area (Fig. 20) four zones within the study site are delineated. The smallest area nearest the west side represents the waterhyacinth coverage ca. 2 weeks prior to the initiation of the study or near the first of October. Coverage at this time was ca. 8.5%. The second, crosshatched area represents the waterhyacinth coverage on 13 October, the day shoots were tagged at the mat fringe. The third and fourth zones (diagonal lines and stippled areas) represent the area of coverage on 27 October and 12 November, or the second and third observation dates. In the two weeks between 27 Oct. and 12 Nov. coverage increased drastically from 41.8% to 73.4% and this tremendous growth was probably due to the increased input of effluent.

Data from the 0.25 sq m samples (Procedure 8) are shown in Figure 83. On 13 Oct., of the 160 shoots per sq m, 73% were injured by S. albugullalis, 30% relatively seriously. By 27 Oct. the average density had increased to 280 shoots per sq m and 95% were injured, nearly 70% were seriously injured. Density increased somewhat further by 12 Nov. to 310 shoots per sq m but S.
Figure 83. Data for randomly selected shoots sampled from 0.25 sq m plots within zone 2 at Coral Springs site 11B. The bars represent the proportion of the plant population injured by S. albiguttalis larvae and the severity of the injury. The line represents average shoot density (per sq m).
albicuttalis declined somewhat to ca. 77% with 42% serious injury. These data were corroborated by that from the tagged plants among which 62, 84, and 88% were injured, in order of respective dates. If the fate of the original 100 individual shoots is followed, 3% were nearly dead on 13 October. Two weeks later, 15 could not be found and 39 had been killed by S. albicuttalis larvae which made up a cumulative 46% of those shoots accounted for. By the last date 25 additional or 64 total shoots had been killed by S. albicuttalis larvae and 4 were lost. Hence, over the 30 day period 81 of the 100 shoots were accounted for and 64 or 79% of these had been killed by S. albicuttalis. This figure could be (and probably is) as high as 83% since most of the shoots that were unaccounted for at this site probably could not be found because they had died.

Data on tagged shoots are compared with that on the untagged, randomly selected 40 shoots in Figs. 84 and 85. The solid lines compare leaf cohort survivorship on subsequent dates and the bars represent the average S. albicuttalis larval injury ratings. In Fig. 84 the first position cohort leaves of the tagged shoots had survivorship values of ca. 84% on 13 Oct. compared to 82% of the untagged plants. On 27 October this declined to 41 and 45%, respectively. By 12 Nov. the tagged plants continued to decline to 25% but the survivorship value of first position leaves on the general shoot population increased to 76%. The same pattern is true if the same leaves are examined over time regardless of position. This is represented in Figs. 84 and 85 by the dashed lines and assume equal leaf production rates by both sets of plants. On tagged plants the youngest leaves which were position one (tag no. 8) on 13 Oct. were technically dead by 27 Oct. since the survivorship value was ca. 50% and by 12 Nov. these were only ca. 25%. On the untagged plants, however, the original 82% survivorship only decreased to ca. 70% by 27 Oct. and to ca. 44% by 12 Nov.
Figure 84. Data from the tagged shoots within zone 2 at Coral Springs site 11B showing the change in leaf cohort survivorship both spatially and temporally and the leaf mortality resulting from *S. albiflora* larval injury. The dashed line represents the survivorship trend for the same leaf cohort over time as position changes.
Figure 85. Data for shoots from randomly selected 0.25 sq m plots presented in the same manner as that for tagged shoots (Fig. 84). The dashed line represents equivalent leaf cohorts over time assuming leaf production rates are the same as those for tagged plants.
Also it may be noted that *S. albiguttalis* larval injury was generally higher on the tagged shoots. This merely serves to point out that even when injury to the plants is extensive, biocontrol may be underestimated if only random samples of plants are examined. Those shoots that die may not be observed and they may be replaced by uninjured shoots. However, both methods are good but they do measure two different parameters. Data from the tagged plants measure leaf and shoot mortality and data from the untagged plants measure the relative condition of the population.

The leaf budget for the second site was remarkably close to that of the first in terms of leaf production with an average rate of 0.109 leaves produced per day. Leaf loss was much higher however at 0.201 leaves per day. Hence, leaves were dying nearly twice as fast as they were being produced and *S. albiguttalis* larvae were almost entirely responsible for this leaf deficit.

A site such as this, one with nutrient rich effluent to serve as a growth medium for the plants, should produce robust, luxuriant waterhyacinth plants with maximum rates of leaf production and the shoots should become large in a very short time. Instead, leaf production rates were slow and plant size remained small in response to the heavy herbivore pressure. In spite of this, the plant population was still able to grow which was evident by increased shoot density and increased area of coverage. On the last observation date, however, it was apparent that the older shoots were dying and this was obvious even in aerial photographs. Plants in the second zone had developed a brown coloration but the population was surviving by virtue of the young shoots in the fourth zone. High nutrient levels at this site probably produced plants which were favored by *S. albiguttalis* but also probably enabled the plants to survive the infestation.
Site 12: Lake Trafford

Sameodes albiguttalis was first found at Lake Trafford in August 1979 on the east side of the lake near the boat ramp. This was the 149th site in the S. albiguttalis dispersal survey (Center 1982a). Twelve waterhyacinth shoots were tagged on 11 August 1981, as described in procedure 6. The shoots were young with inflated leaf petioles, and bore an average of 3.7 leaves per shoot. The average third position leaf length was 15.2 cm. The average plant density was 51 shoots per sq m. Many shoots were damaged by S. albiguttalis and several adult moths were observed. Of the 12 tagged shoots, four were damaged by S. albiguttalis. None of the damage was to the youngest (first position) leaves but was entirely comprised of early instar damage to older leaves. Damage was slight overall and ranged from 5% to 30% mostly on third position leaves. The average leaf condition for positions 1-4 was 98.6, 97.8, 94.6, and 95.4, respectively. Adult Neochetina spp. feeding most affected leaf condition of all leaves except for position 3. Injury caused by Neochetina adults occurred on 8 of the 12 tagged shoots, and four shoots had portions of the leaves missing. None of the shoots were damaged by Neochetina larvae.

On 15 September 81 the South Florida Water Management District was in the process of treating hydrilla with Cutrene. The waterhyacinth mats along the north and west sides of the lake were examined. These plants averaged ca. 50 cm in height. The adult Neochetina feeding was heavy with up to 40% damage per leaf in some cases. No damage by S. albiguttalis was observed. Some of the waterhyacinth mats had broken away from the shoreline and were floating in the middle of the lake and some of these freely floating mats measured 100 x 6:3 feet. Most of the waterhyacinth shoots were tall (50-60 cm) with spindly petioles, they were heavily damaged by Neochetina spp. adults, but were not
damaged by *S. albiguttalis* larvae.

At site 12 on the southwest side of Lake Trafford, three different types of waterhyacinth existed:

1) The type found in the free floating mats as previously described.

2) Small, less than 20 cm tall, lush green in color, inflated petioles, heavily damaged by adult weevils, and growing mixed with type 1.

3) Small, less than 20 cm in height, yellow in color, inflated leaf petioles, growing on top of hydrilla. Damage by adult weevils was slight. Some leaves had no feeding. Many of the petioles were tunneled by *S. albiguttalis* leaving visible "windows."

*S. albiguttalis* was restricted to the third type of plants.

By September, the waterhyacinth mats had shifted, the open water had closed in, and the stakes marking the tagging site could not be found. None of the tagged plants were found and the study was discontinued at Lake Trafford.

Between August and September, however, observations indicated that the *Neochetina* spp. adult population had increased but the *S. albiguttalis* population had decreased.

**Site 13: Wekiva River**

As a result of interference from herbicidal control operations on the St. Johns River at DeLand, sites near there were continually disrupted. To resolve this problem a site was established within the Wekiwa Springs State Park on the assumption that spray operations would not go on within the park. Data were collected only twice before this site was also abandoned. The rapid current and rapid growth of the plants in this area made for difficulties in keeping track of tagged shoots and spray crews did enter the area and treat in the vicinity of the site.
Data were first collected on 21 October 1981 at which time 100 shoots were tagged. On this date shoot density was estimated at 55 per sq m, canopy height was 20 cm, root length was 15 cm, the laminae averaged wider than long at 9.2 by 7.4 cm, and the petioles were quite robust with a maximum width (2.9 cm) more than twice the width of the petiole base (1.3 cm). When the site was re-examined on 18 Nov. 1981 only 18 of the 100 shoots were found. Plant measurements decreased slightly with the canopy height at 16 cm, root length at 12 cm, the laminae measured 8.0 cm wide by 6.1 cm in length on average, and the petiole width averaged 2.8 cm at the widest point and 1.1 cm at the base. Plant density increased ca. 77% to 98 shoots per sq m and the shoots had produced, on average, 4.3 new leaves during the 27 day interim for an average leaf production rate of 0.16 leaves per day. At this rate the initial leaf complement of ca. 5 living leaves would be replaced in ca. 31 days. The number of live leaves increased from 4.9 to 6.8 per shoot as a result of the low leaf death rate (0.10 leaves per day) relative to the high leaf production rate.

*Sameodes albiguttalis* was present in the sampling area on the first examination date and 26% of the shoots were damaged. Shoot injury was classified as minor, however, since the only damage apparent consisted of the "window" type typical of early instar larvae. In November shoot injury had decreased to 16% and most was still considered minor. A fraction of a percent of the shoots was classified as lethally damaged.

Figure 86 illustrates leaf survivorship data for the two dates and the two sampling methods. The solid lines and dark symbols represent shoots which were tagged in October and re-examined in November; thus, the data represent the same plants over time. The dotted lines and open symbols represent the 40 plants subsampled from the 0.25 m$^2$ plots and thus represent entirely
Figure 86. A comparison of data from the Wekiva River showing differences between dates of tagged shoots where the same individuals were examined on each date and of non-tagged, randomly selected shoots where different individuals were examined on each date. Data were adjusted by multiplying leaf condition for each leaf position by the proportion of shoots bearing a leaf in that position. Unadjusted data represent leaf condition only rated on a scale of zero (a dead leaf) to 100 (a live, uninjured leaf). Tagged shoots were distinctly different when they were re-examined because they were older than the general population on average and therefore bore more leaves.
EFFICACY OF SAMEODES ALBIGUTTALIS AS A BIOCONTROL OF WATERHYACINTH (U) ARMY ENGINEER WATERWAYS EXPERIMENT STATION VICKSBURG MS ENVIRONMENTAL LAB
UNCLASSIFIED T D CENTER ET AL. JAN 84 WES/TR/A-84-2 F/G 6/6 NL
different shoots although it hopefully samples the same population. The circles represent the data for 21 Oct. 1981 and the squares that for 18 Nov. 81. The data represent leaf condition weighted for relative frequency of occurrence and as such is indicative of the importance of the leaf cohort in the population. For example, if the condition of leaves in the eighth position cohort averaged 60% but only half of the shoots possessed eighth cohort leaves the 60% would be multiplied by 0.5 to obtain an adjusted value of 30%. This would indicate that eighth position leaves are only 30% as important to the population as they would be if all shoots had them and all were undamaged and entirely green.

It is interesting to note in Fig. 86 that all randomly sampled shoots are very similar. The tagged shoots were randomly selected when they were initially tagged and the 40 subsampled shoots were randomly selected on both dates. On the second date, however, only tagged plants which survived, remained in the area, and could be found were sampled. Hence, these data on tagged shoots on the second date are not random nor representative of the entire population of shoots but rather are representative of the survivors of the population present when the shoots were first tagged. This difference is readily apparent in Fig. 86 in that older leaves are much more important on the tagged plants in November than they were in October or than they are to the population as a whole. This is in spite of the fact that leaf condition unadjusted for relative frequency declined from October to November when compared on a leaf position cohort basis for the cohort four and older leaves (Fig. 86). Hence, although the condition of the leaves decreased, the importance of the older leaves increased.

Very few factors caused significant harm to the plants at this site during this time period. Coots browsed fairly heavily on the leaves and this was probably the most important factor in leaf deterioration. Even so, this affected
only 5-6% of all second through fifth cohort leaves in November. This was one of the few sites where adult weevil injury was not ubiquitous and only 7, 8, 11, 10, and 8% of the first five leaf cohorts, respectively, showed signs of weevil feeding in October and this decreased to 3, 5, 8, 6, and 6%, respectively, in November. Leaf injury caused by weevil larvae never exceeded more than 1% on any leaf position cohort. Both *A. zonatum*, *T. urticae*, and *O. terebrantis* were consistently low. This apparently low leaf injury probably results from the rapid leaf production and resultant quick replacement of injured leaves on the shoot. It was curious that *S. albiguttalis* populations were low at this site since it was the type of area and type of plant form that *S. albiguttalis* normally seems to prefer.

Fig. 87 compares data for leaves that were injured by *S. albiguttalis* with that for leaves that were not injured. As can be seen, leaf condition is reduced 15-35% over all leaf positions. The greatest amount of injury occurs to fourth cohort position leaves but this is probably a cumulative effect over the first four positions. It is important to note that young leaves are affected, which is not the case with most other leaf mortality factors.

**Site 14: West Palm Beach**

This site, which was located in Canal M in Palm Beach County, was the best of the 15 sites in terms of duration, consistency of methods, and meaningful data. The site was comprised of a section of canal ca. 1.4 km long and 15 m wide which had been barricaded at either end to prevent the waterhyacinth plants from floating into or out of that section. When the study was initiated in Dec. 1981, most of the plants were at the western end and a few had drifted downstream and consolidated into a dense stand against the barricade at the eastern end. The central portion was selected as a study area and the plants in
Figure 87. Data comparing average condition of leaves which either had or had not been injured by S. albiguttalis larvae. In October undamaged shoots were deliberately selected and condition of undamaged leaves in November was very similar for equivalent leaf position cohorts. Condition of damaged leaves decreased considerably, however, with the greatest decrease being within the fourth position. Since shoots produced 4.3 leaves the leaf position advanced by that amount between dates. Hence, a leaf in the first position in October would be in the fifth position in November. Fourth position leaves, then, were the first leaves to be produced after the shoots were tagged in October.
this area comprised small scattered patches of loose small shoots which possessed the typical inflated type of leaf petiole.

Figure 88 illustrates the shoot characteristics from 40 shoots which were at first randomly selected from along the edge of the mat. Average shoot size, based upon the length of third position leaves, was initially 11 cm but this progressively increased through September to 42 cm after which a decline appeared to have begun. However, the original study area had closed in by May and access was very difficult, even by airboat. The study area was then moved eastward ca. 100 m and some of the changes in Fig. 86 are the result of this move. Leaf length decreased slightly since the plants were smaller in this area. In fact the largest shoots were present at the west end, nearest the nutrient source, and they progressively decreased in size towards the east causing the mat to have a tapered appearance. As water flowed under the mat those shoots upstream removed nutrients leaving less for those downstream. Hence, when the study site was moved it was moved to an area with lowered nutrient concentrations and this was apparent in the plant measurements. Even though shoot size showed little change it should have increased. Root length increased dramatically in relation to shoot size which is generally a sign of lower nutrient (usually nitrogen) availability. The size of the laminae decreased a great deal since those downstream were not as luxuriant as those upstream. Petiole shape appeared to change very little. Although the site was moved to an area of more open water, the plants were not the typical, small, fringe-growth type with inflated petioles but were more the tall slender type which had broken free from the upstream population forming loose colonies within this open area.

In May a large cutter barge was used to chop up the waterhyacinth in the canal system around the Loxahatchee Marsh to the west of the study site.
Figure 88. Data from site 14, Canal M, near West Palm Beach showing morphometric characteristics of the waterhyacinth shoots within the study area. The break between April and May is due to the necessity of changing sampling locations. The data show the change in plant type from the small, inflated petiole, colonizing form to the taller, elongated petiole, competitive form. These data are means of 40 shoots selected randomly from 0.25 m² samples (4 shoots from each of 10 samples derived monthly).
Several weeks were required to complete the job and by the time observations were made in June most of the leaves which had been chopped up had decayed. This almost certainly caused a release in nutrients at that time which may explain the decrease in root length by 22 June. It must be noted, however, that the cutter did not harvest the plants but merely chopped them up. This was done at great expense (ca. $8000), and it cleared only 19 km of canal. By 11 March most of the plants had been cut up but by 7 April they had begun to recover and reinfested nearly the entire 19 km. By 11 May, they had completely recovered, were deep dark green and healthy and it could not be discerned that any control measure had been applied.

In July, the shoots within the study area began to transform. Lamina length increased and began to exceed lamina width indicating that the shape of the laminae was in the process of changing to a more lanceolate form. The width of the petioles decreased, especially when the diameter at mid-length is considered relative to basal diameter. Root length and shoot length became nearly equal and remained so through October but in November leaf length decreased relative to root length.

Figure 89 illustrates data for the tagged shoots showing the average degree of \textit{S. albiguttalis} larval injury and the survivorship value for each leaf position cohort. On 23 December 1981, the shoots were in quite good condition with an average of over six live leaves and \textit{S. albiguttalis} larval injury was slight and confined to the older leaves. By January shoot condition decreased slightly as leaf injury caused by \textit{S. albiguttalis} larvae increased somewhat and affected younger leaves. Still, however, it was mainly confined to the older leaves. Damage continued to increase and overall leaf cohort survivorship to decrease through March at which time a great deal of injury (16\%) was localized in the youngest leaves. Although injury caused by \textit{S. albiguttalis} larvae decreased
Figure 89. Data from tagged shoots showing the spatial distribution of S. albiculata induced leaf injury, comparing leaf survivorship among leaf position cohorts (age classes), and showing the changes in these from month to month. The letters on the lines simulate leaf tags and the dashed lines show changes in the same leaf cohorts over time.
in April, leaf cohort survivorship did not improve. Data for late May again showed light *S. albiguttalis* induced leaf injury which was confined primarily to old leaves.

In Figure 89 leaves indicated with the same letter and connected by dashed lines represent the same leaf cohorts showing their change in position on subsequent dates. Further leaf production data are presented in Figure 90 which shows an average leaf budget for shoots at this site. As can be seen, over the long term, leaf death was exceeding leaf production resulting in a slow gradual decline in the number of live leaves per shoot. Although leaf production rates were not constant, the average rate over the year was 0.114 leaves per day, or in other words, a new leaf was produced ca. every 8.8 days. A leaf died, however, on the average of every 8.0 days and, as a result, the number of live leaves per shoot declined from ca. six to only four over the year.

Data from non-tagged shoots which show the percentage of shoots injured by *S. albiguttalis* larvae are presented in Fig. 91. Early in the year most shoot injury was considered to be minor but by April the number of shoots fatally injured by *S. albiguttalis* larvae greatly increased. All *S. albiguttalis* activity ceased by July and remained at a very low level throughout the remainder of the year. The solid line in Fig. 91 shows the shoot densities that the injury frequencies are based upon. It should be noted that the percentage of shoots severely injured increased at the same time shoot density increased. This was also the time during which the plants were changing form. We suspect that this heavy damage is associated with a high proportion of mature larvae present in the plants at that time. These were from eggs laid at an earlier date when the plants were different. After that generation was completed, however, the plants were no longer suitable for oviposition and the insects failed to re-infest.
Figure 90. A leaf budget for shoots at site 14. The regression line with closed dots represents the average total number of leaves produced per shoot and the open dots represent the number of live leaves per shoot for the tagged shoots. The bars represent the average number of live leaves per shoot on the 40 untagged shoots. The triangles and included regression line represent the cumulative number of leaves which died and are estimated by calculation (initial no. live leaves + no. new leaves - present no. live leaves) using leaf production data from tagged shoots and live leaf data from untagged shoots.
Figure 91. Data from ten 0.25 m² waterhyacinth plot samples showing the shoot density on each sampling date, the proportion of the shoots with symptoms of *S. albiflora* larval injury, and the severity of that injury. The injury was considered lethal if the apical bud was destroyed and the shoot was no longer capable of growing. Critical injury was comprised of considerable damage especially to the younger leaves but the apical bud uninjured. Damage to old leaves with no symptoms of young leaves and no possibility of apical bud injury was considered minor.
Data which show the spatial as well as the temporal aspect of the *S. albicuttalis* infestation are presented in Fig. 92. As noted earlier, the infestation was never intense and in December was barely evident. In March *S. albicuttalis* induced leaf injury was still low, generally less than 10% per leaf but was uniformly distributed throughout the shoots. In April damage to older leaves had decreased and was concentrated in the youngest leaves which, again, is indicative of an insect population of predominantly late instars. By May damage was confined primarily to the older, dead leaves which indicated that this was the remaining signs of a past infestation and that the shoots had outgrown the damage. From June onward *S. albicuttalis* larvae were essentially non-existent.

While the *S. albicuttalis* larval population at this site never achieved damaging levels, this was not true of the *Neochetina* spp. larvae. Because the waterhyacinth population sampled was relatively recent, weevil larval numbers were low early on because of insufficient time for an infestation to build up (Fig. 93). In the winter and early spring weevil larval induced leaf injury was low and restricted to older leaf cohorts. In May, however, a buildup began and the larval damage began to appear in younger leaves. Not only did the frequency increase but so did the severity. Peaks in activity of weevil larvae occurred in May-June and again in August. The infestation clearly began in the older leaves and moved towards the younger leaves by the end of the year.

No other factors were sufficiently intense to cause severe injury to the shoots. Spider mites were present early in the year but injury symptoms were apparent only on old leaves indicating that this was the remnant of an old infestation (Fig. 94). After March, spider mites disappeared and a light infestation reappeared briefly in August. Otherwise, spider mites were not a factor in leaf mortality.
Figure 92. Data showing the average amount of injury to leaves on the 40 non-tagged shoots caused by S. albistalalis larvae. The data are represented on an intra-shoot spatial scale in which the numbers 1-12 represent the leaf position cohorts or age classes of the leaves. The illustration is set up to show the change in the amount of damage in each leaf position over time.
Figure 93. Same as Fig. 92 but data showing the average amount of leaf injury caused by weevil larvae.
Figure 94. Same as Fig. 92 but data showing leaf injury due to spider mites.
The temporal and spatial distribution of waterhyacinth mite induced leaf injury is presented in Fig. 95. As with weevil larvae and spider mites, early signs of injury were present only on old leaves. Leaf replacement caused this to diminish from January through March but a light infestation began in April and built up through June. This tapered off through the summer and became very rare by October. Again, these mites were never a significant factor in leaf mortality.

The leaf injury caused by weevil adults is shown in Fig. 96. No spatial pattern of feeding injury was ever apparent within the shoots. This was due to the fact that the adults preferentially feed on young leaves and the persistent lesions which result carry through as the leaves age. The temporal pattern of leaf injury was one of a gradual buildup through the year which became most intense in the fall. It never became severe, however, and weevil adults were not yet a significant leaf mortality factor.

The only plant pathogen which was prevalent at this site was the zonal leaf spot fungus, Acremonium zonatum. Spatially, it was almost always confined to the oldest leaves and, temporally, it was most prevalent in the spring and fall. Data are shown in Fig. 97.

Data comparing leaf survivorship among cohorts over time are presented in Fig. 98. Generally, leaf survivorship was greatest from December through February, especially among the younger leaf cohorts. This was due to the absence of any significant leaf mortality factors at that time. Survivorship declined through April as S. albiguttalis larvae inflicted increasing mortality to young leaves. As S. albiguttalis declined in May, however, survivorship began to improve until August when weevil larvae began to have an impact. Leaf survivorship generally declined thereafter.

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Figure 95. Same as Fig. 92 but data showing leaf injury due to waterhyacinth mites.
Figure 96. Same as Fig. 92 but data showing leaf injury due to adult weevils.
Figure 97. Same as Fig. 92 but data showing leaf injury caused by zonal leaf spot fungus.
Figure 98. Data showing the change in leaf cohort survivorship over time. Leaf survivorship represents the average relative frequency of each leaf cohort in the population multiplied by the average condition of leaves of each cohort, the product multiplied by 100. Note that the leaf position scale is the opposite direction when compared to Figs. 92-97.
If Figs. 92 through 97 are examined, a succession of infestations by the various agents can be seen and these are temporally distinct. Spider mites occurred first being the predominant factor in January and February. *S. albiguttalis* followed and was most prevalent in March and April. Weevil larvae began to become predominant in May and were accompanied by an increase in zonal leaf spots. Waterhyacinth mites briefly appeared in June but were never predominant. Weevil adults were most prevalent in late summer and fall. Only *S. albiguttalis* larvae and weevil larvae had a significant impact on leaf survivorship.

As mentioned earlier, 100 shoots were tagged on 23 Dec. 1981. Of these 100, 49 were lost and unaccounted for at the end of the year. Of the remaining 51, 16 or 31% had been killed by *S. albiguttalis* larvae, 22 or 43% had been killed by weevil larvae, and 13 or 25% were alive after more than a year. Data on shoot survival and mortality are presented in Fig. 99. The greatest decrease in shoot survival occurred during March and April and was directly attributable to *S. albiguttalis* larval injury although weevil larvae certainly contributed to this. A second period of shoot mortality occurred in August which was entirely due to weevil larvae. Shoot mortality did not seem to occur constantly but rather increased in steps. Why this would be true is unknown at this time.

Data on leaf production also show some interesting trends. When only shoots with no *S. albiguttalis* larval injury are included an average of 43.8 leaves were produced per shoot over the year. When only shoots with minor *S. albiguttalis* larval injury are included, the number of leaves produced is nearly the same at 44.6 leaves per shoot. However, when all injured shoots are included, regardless of the degree of damage, then each shoot produced only 25.1 leaves per annum. The 11 shoots that were seriously injured only produced 5.2

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Figure 99. Data showing the trend in shoot survival (open dots) and the percentage of shoots killed by either *S. albipalpis* larvae (solid dots) or *Neochetina* spp. larvae (triangles). Data are based upon the original 100 shoots tagged on 23 Dec. 1981 excluding those which were lost or otherwise unaccounted for. Note that only ca. 25% of the shoots survived the year and most of those that died were killed by either *S. albipalpis* larvae or weevil larvae.
leaves before they died. Hence, these data suggest an all or none effect by *S. albiguttalis*. They do not slow down rates of leaf production and unless the infestation is fatal to the shoot, it will replace the damaged leaves and recover from the injury. The stress associated with the insect damage may result in the production of smaller leaves but not fewer leaves. Leaf production seems to be independent of all but environmental effects. The effect of *S. albiguttalis* is manifested in shoot mortality and *S. albiguttalis* larvae, weevil larvae, desiccation, and frost are the only natural factors which we observed directly killing shoots.

**Site 15: Cypress Creek Canal**

This site, in many ways, turned out to be one of the best in terms of evaluating *S. albiguttalis* efficacy. The plants were located along the banks of the Cypress Creek or C-14 canal and were small, free-floating, and loose. One hundred shoots were tagged on 28 Jan. 1982 but they tended to drift away as wind or waves moved them from the bank towards the center of the canal. Therefore, a floating barricade was constructed of PVC pipe and attached to the bank to act as a corral and retain the plants within the study area. This tended to work well although the backwash from the bank that resulted from the wake of power boats occasionally washed the shoots over the barricade and some were lost.

The 100 shoots which were tagged were selected randomly and, on 28 Jan 1982, 25 of them were seriously injured by *S. albiguttalis* larvae and appeared to be dying. These, in fact, did die before the next observation on March at which time an additional 24 were found to have been killed and 27 had been lost. Thus, within 33 days, of the 73 shoots which could be accounted for, 49 or 67% had been killed by *S. albiguttalis* larvae. By 2 April 1982 an additional five had died from *S. albiguttalis* injury, two from weevil larval injury and 11 more
were lost. The cumulative totals by this date were 62 accounted for, 38 lost, and 54 or 87% of those accounted for dead due to *S. albignuttalis* larvae. Although these plants were continually checked until early July, the numbers changed very little. By that date no more of the shoots had been killed but an additional seven were lost and none of the original 100 shoots remained.

Of the 100 shoots which were initially tagged in January, only two survived to June. One of these two had only moderate *S. albignuttalis* injury to fourth through sixth position leaves on 28 January but the production of six new leaves essentially negated this injury by 2 March. This was true in spite of the fact that reinfection of the shoot occurred. Leaf positions seven through nine showed moderate to high injury whereas these were formerly positions one through three and uninjured. Position six was also injured and this was a new leaf since the last observation. However, the first five leaf positions were uninjured by *S. albignuttalis*. By April the shoot had produced seven new leaves and the first nine were free of *S. albignuttalis* damage.

The second shoot which survived to June had only minor damage to leaf positions four and five on 28 Jan. The leaf which was in the first position was dead by 2 March as a result of *S. albignuttalis* larval injury but, by that time, the shoot had produced five new leaves and the dead leaf was in the sixth position. By April the second youngest leaf (position two) was nearly dead from *S. albignuttalis* larval injury but the first position leaf was unharmed. By this date the production of eight new leaves had negated the effects of the previous injury. By 4 May the shoot had produced five new leaves, the injured second position leaf was in the seventh position, the first six leaf positions were unharmed, and no subsequent injury occurred.

This same pattern was seen on other shoots but, in most, as the shoot pro-
duced leaves the *S. albiguttalis* larvae were able to move, kill the first position leaves, and destroy the apical bud in the process, and thus kill the shoot. Clearly, if this did not happen the shoot could rapidly outgrow the effects of the damage by replacing the injured leaves.

Of the 57 shoots accounted for, only 12 were alive on 2 March, the remainder had been killed by *S. albiguttalis* larvae. Of the 12 alive in March, four had produced no leaves, one had produced two leaves, two had produced three leaves, two had produced four leaves, one had produced five leaves, and two had produced six leaves. Of the 45 dead, only one had produced one leaf. By 2 April only two shoots were alive and these had produced seven and eight leaves and were of the shoots that had produced six and five leaves, respectively, the month before. By June, these two shoots had produced a total of 23 and 24 leaves, respectively, or a new leaf every 5 days. None of the other shoots produced more than 9 leaves over the 125 day period before they were stopped by *S. albiguttalis*.

As shoots died or were lost, other shoots were tagged in order to retain ca. 100 tagged individuals within the study area. In all, 185 shoots were included between 28 Jan. and 6 Aug. 1982. Of these only the 54 of the initial 100 shoots died from *S. albiguttalis* injury but five were killed by weevil larvae, 116 were lost, and ten remained at the end of the study. Thus, of the 69 shoots accounted for, 78% were killed by *S. albiguttalis* larvae, 7% by weevil larvae, and 14% survived.

Data in Fig. 100 show a change in characteristics of the shoots in the waterhyacinth population at this site. These data represent measurements from 40 randomly selected shoots and not from the tagged shoots, but a similar trend was noted in both sets of observations. In January the typical small, robust
Figure 100. Data showing the average morphometry of waterhyacinth shoots at site 15 near Palm-Aire Broward Co. The top figure shows the diameter of the petioles at the mid-point as compared to the base. The convergence of these lines is indicative of the loss of the inflated type of petiole and the transformation to the more linear form. The middle figure represents the length of the lamina relative to the width. When width exceeds length the shape tends to be reniform whereas when length exceeds width the shape tends towards lanceolate. The bottom figure represents the extent of shoot development (leaf length) relative to root development. Small leaves and an extensive root system tend to be indicative of shoots limited by nutrient availability. The reverse tends to occur under conditions of intense intra-shoot competition for light and space.
shoot with inflated leaf petioles was present. This is apparent from the leaf measurements which show petioles much wider at mid-length than at the base, laminae which are wider than long, small shoot size, and well developed root system (roots longer than leaves). Plant form gradually changed, however, and by May leaf length exceeded root length, by June the petiole diameter at mid-length was about equal to that at the petiole base, and by August the laminae were nearly as long as wide. Between April and June the canopy nearly doubled in height based upon the length of the leaves. It is interesting to note in Fig. 101 that the percentage of shoots injured by *S. albiflattalis* larvae declined as did plant density. Density most likely declined in response to shoot size, however, and not as a result of the insect damage.

The assessment of *S. albiflattalis* effects from the tagged shoot data is more or less confirmed by the data from the ten 0.25 sq m samples, presented graphically in Fig. 101. In January 76% of the plants showed symptoms of *S. albiflattalis* injury and 33% were damaged so extensively that they were expected to die. This compares with 25% of the tagged shoots. Overall injury increased somewhat in March with 81% injured but lethal damage decreased to 29%. Those previously assessed as fatally injured probably died and this 29% represented new damage. This compared to 33% of the original 100 tagged shoots. By April total damage decreased to 35% and fatal injury to only 10% which compared well with the 8% (five out of 62) noted from the tagged shoots. Damage was very low thereafter but seemed to be on the rise again in August when the study was ended. The decrease in *S. albiflattalis* activity again seemed to be closely linked to the change in plant form and possibly to the warmer summer weather.

Data from the tagged plants showing relative *S. albiflattalis* larval injury to each leaf position cohort and cohort survivorship are presented in Fig. 102.
Figure 101. Data showing the proportion of the waterhyacinth shoots injured by *S. albipunctata* larvae and the severity of that injury over the course of the study. The line represents shoot density based upon an average of ten 0.25 sq m samples.
Figure 102. Monthly data for tagged shoots showing the relative survivorship of each leaf position cohort (lines) and the average rating for leaf injury caused by S. albiguttalis larvae. The encircled numbers and dashed lines represent the same group of leaves and show the change in survivorship over time.
In late January *S. albiguttalis* injury was relatively evenly spatially distributed and shoots were in poor condition. Only the first three cohorts were considered alive. By early March shoot condition deteriorated further and damage to the younger leaves increased. Leaves previously in the first position were mostly fourth position and survivorship had decreased from 66% to 50%. *S. albiguttalis* injury increased over all leaf positions except three and four. By early April *S. albiguttalis* injury decreased overall and survivorship of the first four leaf position cohorts increased dramatically. This recovery of the leaves and decline in *S. albiguttalis* injury continued through June.

Data for leaf budgets are presented in Fig. 103. Leaf production proceeded at an average rate of 0.15 leaves per day although the curve for leaf production was sigmoidal (dotted line) rather than linear (solid line). Leaf death occurred at an average rate of 0.14 leaves per day so the leaf complement showed slight net gains in live leaves. Data from non-tagged plants, however, showed a decline in the number of live leaves after April. This was due to the inclusion of younger shoots in the sample rather than an increase in leaf death, whereas the tagged plants are generally the same plants time after time and this method is less likely to sample younger shoots.

Data for condition of non-tagged shoots (Fig. 104) differ from that of tagged shoots. The data for late January and early March show the plants in relatively poor condition and this corresponds with the data for *S. albiguttalis* injury (Fig. 105). Shoot condition improved markedly in April but declined again later in the year. This decline coincided with leaf injury caused by weevil larvae (Fig. 106).

In summary, *S. albiguttalis* was most abundant at this site during late winter, a phenomenon noted at other sites. If the youngest leaf of severely
Figure 103. A leaf budget for tagged shoots at site 15 near Palm-Aire. Note that although a linear regression was useful for estimating an average rate of leaf production, the curve was actually sigmoidal increasing in April and May as S. albivittalis larval damage declined. The bars represent the average number of live leaves per shoot on non-tagged shoots.
Figure 104. Data for non-tagged shoots showing the relative leaf cohort survivorship on subsequent months in 1982. Note that shoots appeared to be in the best overall condition in April. In January and February young leaves were in poor condition. From June onward condition of all cohorts declined but this was markedly so in older leaves.
Figure 105. Data comparing relative extent of S. albipalpis larval injury among leaf cohorts over time. Note that the high damage to young leaves corresponds to low survivorship of young leaves in Fig. 104.
damaged shoots was completely destroyed by *S. albiguttalis* larvae, the shoot usually ceased leaf production and subsequently died. Shoots in this condition rarely persisted for more than one month after these injury symptoms became apparent. If the extent of injury was not sufficient to stop leaf production, the shoots always recovered. *Neochetina* spp. larvae increased and began to seriously impact the shoots shortly after they had begun to recover from the *S. albiguttalis* infestation. Hence, plants at this site were constantly under rather intense pressure from biological control agents. None of the other natural enemies were ever sufficiently intense to become damaging to the shoots.
DISCUSSION

An understanding of the effects of biological agents upon a plant first requires an understanding of the plant itself. In particular, population parameters must be known so that the effects of herbivores and disease can be assessed. This requires estimation of rates of growth, turnover, etc. Unfortunately, most studies rely on changes of state variables, such as plant size, and standing crop, and thereby overlook the dynamics of herbivore-plant interactions.

In the case of waterhyacinth, the whole plant is a difficult entity to study. Floating plants, unlike rooted species, do not stay in one place but rather drift away and may be difficult to locate from one time to the next. Further, the sympodial branching produces an organizational pattern consisting of a parent shoot with several offsets all connected by fragile stolons (see Fig. 107). Harper (1977) classifies the whole plant as a genetic unit or "genet" and the vegetatively produced, genetically identical offsets as "ramets". A waterhyacinth genet may fragment into its component ramets if the interconnecting stolons deteriorate or break. Thus, what was once a single plant may then become several and the integrity of the unit obfuscated.

The ramets, or individual shoots, seem to be the basic component units in waterhyacinth populations and these are often the subject of evaluation. Certain difficulties are inherent in this approach, however. When a ramet is produced at the axillary bud of the parent plant, at first only a small primary leaf is present (see Fig. 1). As the stolon elongates the ramet begins to produce the normal type of leaf but the stem is very small and the root system poorly developed. In fact, the roots may not be at all apparent or only evident as small bumps (initials). Further growth eventually results in a complete...
Figure 107. A diagrammatic illustration of a waterhyacinth plant (genet) showing the geometrical arrangement of offshoots (ramets) in a clonal hierarchy, each connected to its parent shoot by a stolon. The dashed line represents a stolon which has deteriorated; thus, what is actually two parts of one plant may appear to be two plants or up to 21 plants if each shoot eventually becomes separated. The diameter of the circles around each shoot is proportional to the age of the shoot in a relative manner.
plant with all of its component parts, but it is often difficult to define the point at which the offset becomes a discrete entity. Further, it may be necessary to distinguish between ramets attached to the parent by a stolon and those separated after the stolon breaks or deteriorates.

In population studies, it is desirable to determine the age structure of the population. Early in the life of a ramet this is determinable because it progresses through identifiable, discrete stages including a primary leaf stage, a one leaf stage, a two leaf stage, and so on. As the ramet matures, however, leaf production and senescence reach a steady-state and the number of leaves on the stem changes slowly or not at all. The lower end of the stem decays and is replaced by new growth at the upper end. At this point, the age of the ramet is not easily ascertained. Also, in population studies, it is necessary to know if and when the basic population unit dies. It is difficult to determine if a ramet is dead since, although it may have no living leaves, it could ultimately resprout and continue to grow.

Through experience, we have found that the best unit to use in waterhyacinth population studies is the individual leaf. Several reasons exist for this conclusion and these are examined in detail in Center (1981c). The advantages of studying leaves are as follows:

a) A leaf is a clearly identifiable structural unit.

b) Since leaves are produced singly at the stem apex and at regular intervals, the age structure of the leaves is readily determined (see Fig. 108).

c) Leaf production occurs at predictable and easily measured rates.

d) Leaves are conspicuous organs and the most obvious feature of the plant and often comprise the bulk of the biomass.
Figure 108. A waterhyacinth stem (rhizome) showing the spiral arrangement of the leaves as they are produced at the apex. The younger leaves occupy stem positions with smaller numbers whereas larger numbers represent stem positions of older leaves. Position only appears to change as the leaves age and this apparent change is due to stem elongation at the apex. This illustration is very diagrammatic and leaves are not drawn in proportion with the stem. Only the leaf petioles are shown, the laminae are not...
e) Factors which damage or kill leaves are easily diagnosed.
f) Biological control agents all feed upon or otherwise infest the leaves and affect leaf production and turnover.
g) Leaves have a distinct life cycle proceeding from the time they erupt from the bud to the time they senesce and are ultimately sloughed from the stem.
h) Leaves are easily tagged for repeated observation.
i) Leaf age distributions are relatively stable.

As with everything, however, there are disadvantages to studying leaves.

These are as follows:

a) When plants are rapidly growing, tagged leaves may be sloughed before the site is re-examined. Plants may therefore require frequent observation and re-tagging.

b) Plants with tagged leaves may not be recovered, in which case the fate of the plant (or leaves) is not determinable. It may have died, outgrown the tags, or merely drifted away.

c) The process of tagging and repeated examination may adversely affect the plant and provide biased data.

d) Studying tagged plants may restrict the study to those plants that were present when the initial tagging was done. In some cases, new shoots are continually produced and these may not be included in the study unless new plants are repeatedly tagged. Continually increasing the number of plants to be evaluated, however, may result in the study becoming unwieldy and unmanageable. Nonetheless, the new shoots may be of utmost importance in the evaluation.

e) The point of death of a leaf is not always clear. A leaf should be
considered dead when it is no longer functional. The leaf gradually senesces, however, and death must be subjectively determined.

It is clear that population studies of waterhyacinth leaves can provide a great deal of useful information but may not provide all the information needed for a proper evaluation. A combined approach is necessary. Harvesting studies provide the best data for documenting changes but leaf production studies provide insight into the dynamic process of change.

The interested reader should refer also to Abul-Fatih and Bazzez (1980); Carpenter (1980); Harper (1977, 1981); Nobel et al. (1979); and Sagar and Mortimer (1976).

Life Tables as a Tool for Evaluating the Leaf Population Dynamics of Waterhyacinth

Life tables (or survivorship tables) have a long history of use in the insurance business for actuarial purposes as a means of computing annuities. Deevey (1947) was perhaps the first to recognize the utility of life tables as a means of analyzing the growth of animal population in nature although others (e.g. Pearl et al. 1941) had earlier applied these techniques to the analysis of laboratory populations. Since that time, life table analyses have been used most extensively in animal population biology, especially in the analysis of insect populations. Harcourt (1969) and Varley and Gradwell (1970) have reviewed the subject in great depth.

Few attempts have been made to study the demographics of plants by way of life table analyses. Notable among these are the studies by Hett and Loucks (1971), Hawksworth (1965), Namkoong and Robards (1974), and Harcourt (1970). The interested reader should consult the reviews by Harper and White (1974) and Harper (1977). A particularly interesting example from the paper by Harcourt
(1970) is his use of crop life tables to assess economic losses resulting from mortality factors by converting population parameters to monetary values. This approach yields useful cost-benefit data for pest management practices in agricultural crops in which the objective is to decrease the impact of mortality factors. It immediately becomes apparent that, in weed management, life tables could be used to determine the value of mortality factors which affect the target plant and the objective becomes to increase the impact of these factors. The resultant monetary figures could then be used to compare the cost-benefit of various control approaches.

Two types of life tables are often constructed. The first type is based upon data obtained by observing the successive mortality of individuals in a population as they increase in age. This is the age-specific, or horizontal, or dynamic life table. The second type assumes a stable age distribution and is based upon the age structure of the population at a point in time and infers death rates from the decline in numbers of successive age classes. This is the time-specific, or vertical, or static life table. Discussions of the types of life tables and their limitations and applications can be found in Krebs (1972), Southwood (1975), Dempster (1975), Deevey (1947), and others.

Several parameters are associated with life tables, the first of which is the parameter $x$ which represents the age class or cohort for the interval considered. The number surviving at the beginning of the interval is denoted $l_x$ and the number dying during the interval is denoted $d_x$. The rate of mortality expressed as the number dying as a proportion of the number entering the age interval is denoted $q_x$. The mean expectation for further life for those alive at the beginning of the interval is $e_x$ and is the ratio of $T_x/l_x$. The parameter $T_x$ is the average number alive per cohort ($l_x$) summed over all cohorts.
A specific mortality factor is usually referred to as a function, abbreviated $d_xF$. In studies of leaves a further parameter must be considered which we will refer to as leaf "condition" ($c_x$). An animal cannot be partially dead but a leaf can be. The parameter $c_x$, therefore, merely represents the average proportion of the individual leaf which remains alive. Therefore, $l_x$ represents a value for the number present at the beginning of the interval ($n_x$) weighted for the average leaf condition ($c_x$) by deriving the product of the two ($l_x = n_x c_x$). Thus a value for $l_x$ of 0.64 could indicate that 64% of the leaves were present and all were 100% alive, or 100% of the leaves were present but averaged only 64%, or 80% of the leaves were present and their average condition was 80%, etc. In this case, if the $l_x$ value for the next cohort is 54% then $d_x$ (for the first cohort) is 0.10 indicating an additional 10% mortality. Thus, the life table is actually a leaf budget for successive cohorts where losses are ascribed proportionally to various agents of mortality such as insects, disease, and frost.

Table 2 presents a time-specific life table for all of the plants examined from 0.25 m$^2$ samples from all sites over the term of this study. Table 3 lists the $d_x$ values for each $d_xF$ on each cohort. Examine the lines for cohorts 6 and 7. Note the number of leaves present ($n_x$) changed from 870 to 699 indicating a loss of 171 leaves. The leaf condition ($c_x$) changed from 49.9% to 38.4% or 11.5%. Thus $l_x (n_x c_x)$ changed from 434 to 268. The effects of mortality factors in this study, however, were based only upon $c_x$ and represented cumulative effects. For example, adult weevil feeding accounted for ca. 8% of the total 71.6% deterioration in average leaf condition from cohort 1 to cohort 7. This must be converted in such a manner as to determine the effects of weevil feeding upon the cohort 6 leaves only. It can be determined that weevil
Table 2. Time-specific life table analysis for waterhyacinth leaf mortality. The data represent averages based on plants collected throughout Florida and during all seasons and, as such, represent a hypothetical "average" population of leaves.

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<th>LEAF POSITION COHORT (X)</th>
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<th>C_x</th>
<th>I_x</th>
<th>d_x</th>
<th>1000</th>
<th>q_x</th>
<th>e_x</th>
<th>L_x</th>
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Table 3. Mortality factors (dxF) for leaves from Table 2 with contributions of each dxF to mortality rates of each cohort. Numbers are number dying of the 1160 base population.

<table>
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<th>2-3</th>
<th>3-4</th>
<th>4-5</th>
<th>5-6</th>
<th>6-7</th>
<th>7-8</th>
<th>8-9</th>
<th>9-10</th>
<th>10-11</th>
<th>11-12</th>
<th>12-13</th>
<th>TOTAL</th>
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<td>4</td>
<td>25</td>
<td>20</td>
<td>18</td>
<td>11</td>
<td>8</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Neochetina adult</td>
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<td>3</td>
<td>15</td>
<td>11</td>
<td>9</td>
<td>5</td>
<td>3</td>
<td>2</td>
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<td>Zonal Leaf Spot</td>
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<td>0</td>
<td>2</td>
<td>4</td>
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<td>9</td>
<td>6</td>
<td>3</td>
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<td>1</td>
<td>4</td>
<td>6</td>
<td>8</td>
<td>6</td>
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<td>0</td>
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<td>0</td>
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<tr>
<td>Partial Leaf</td>
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<td>1</td>
<td>11</td>
<td>10</td>
<td>13</td>
<td>10</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>0</td>
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<td>2</td>
<td>26</td>
<td>38</td>
<td>60</td>
<td>68</td>
<td>56</td>
<td>37</td>
<td>28</td>
<td>10</td>
<td>7</td>
<td>1</td>
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<td>Total (dX)*</td>
<td>235</td>
<td>31</td>
<td>17</td>
<td>134</td>
<td>135</td>
<td>173</td>
<td>167</td>
<td>119</td>
<td>70</td>
<td>49</td>
<td>14</td>
<td>10</td>
<td>1</td>
<td>1155</td>
</tr>
</tbody>
</table>

* Values of dX may not agree with Table 2 due to rounding error.
feeding comprised ca. 11% of the total leaf damage, the change in $I_x$ was a loss of ca. 77% so weevil damage contributed ca. 2% to $d_x$ for cohort 6 (i.e. 11% of 77%). Summing these values for all $d_x$ the total $d_x$ for cohort 6 is 166 or a 15% increase in total mortality. Subtracting the $d_x$ for cohort 6 of 166 from the $I_x$ of 434 yields 268 which is the $I_x$ for cohort 7. Dividing the $I_x$ for cohort 7 by that for cohort 6 yields the proportion of cohort 6 surviving ($S_x$) which, in this case, is 62%. Carrying through the calculations as described earlier, the expected life ($e_x$) for cohort 6 leaves is an additional 2 leaf position cohorts. In other words, leaves which survive to cohort 6 can be expected to live to cohort 8, on average.

It should be obvious that not all leaves are of equal importance to the plant. In order for a leaf to produce photosynthate and thereby contribute to the energy demands of the plant body, it must remain healthy. The older a leaf is the less likely it is to contribute to the plant and the less remaining life it has to do so. The importance of a leaf cohort should be proportional to the area under the survivorship curve (Fig. 109) beyond that cohort and this value is equivalent to $T_x$. If the data represented observations over time this value would be leaf-days but in the time-specific case we will refer to this as leaf-cohort duration.

It should be equally obvious that the more important biological control agents are those that reduce leaf-cohort duration the most, i.e. those that affect survival of the youngest leaves. In the example (Fig. 109), most mortality factors, such as pathogens and mites, only affected old leaves which were near the end of their life expectancy, introduced biological control insects were essentially the only factors affecting young leaves (i.e. cohort 1). If it is assumed that neither $S$. albifutalis nor Neochetina spp. were present and the
life table data recalculated accordingly, the survivorship curve represented by the dotted line in Fig. 109 results. In this case a new leaf has a life expectancy \(e_x\) of 7.3 cohort positions whereas otherwise the \(e_x\) was 5.4. Leaf cohort duration increased from 5600 to 8467 indicating that the insects accounted for a 34% reduction. This, then, represents a good estimate of the degree of control attributable to the introduced biological control agents.

The Intra-Shoot Spatial Distribution of Leaf Injury on Waterhyacinth

Since the spatial distribution of waterhyacinth leaves on the stem is a function of time, then the spatial distribution of leaf injury is also temporal. Therefore, depending upon whether an agent which damages leaves does so randomly or whether it selectively attacks leaves based upon age or spatial arrangement, the pattern of damage on the plant will vary spatially. If leaf injury is random, that is if all leaves on the shoot are equally susceptible, then symptoms should increase in a linear fashion from younger to older leaves. This is because injury would be directly proportional to time of exposure. The chance that a leaf would be attacked would increase the longer the leaf is available and older leaves would have been available longer. Hence, even though the injury is random, a distinct spatial (temporal) pattern should be apparent.

If the agent causing leaf injury selectively attacks young leaves, then the injury to those young leaves should carry through, but not increase, as they age. In other words, there should be no apparent relationship between leaf position (or age) and injury intensity. The leaves would be susceptible for only a short time and then not be harmed further.
Figure 109. Life table data from all plants examined from the 0.25 m² samples averaged by leaf position cohorts over all dates and all sites. Line A shows the trend in survivorship as leaves age and the bars represent the mortality factors responsible for decreasing survivorship. Line B represents calculated survivorship after mathematically removing and re-distributing leaf mortality caused by S. albicutalis larvae and Neochetina spp. larvae and adults. The result is a 50% increase in survival which indicates that these factors reduce leaf longevity by ca. 34%, primarily through the destruction of young leaves.
If only old or "middle-aged" leaves are attacked, the pattern should be one where injury rapidly increases at one point within the shoot and levels off thereafter. In this case the shape of the increase would be dependent upon the degree of preference (the fastidiousness) of the agent and the duration of persistent attack.

These three patterns of leaf injury (random, young leaf preferred, or old leaf preferred) are basic and over-simplified and obviously many other patterns can be envisioned which are caused by semi-random events. For example, some agents seem to prefer certain leaves but will also feed randomly to a lesser extent. Also, agents such as *S. albiguttalis* may stop the process of leaf production by feeding upon the youngest leaf and destroying the adjacent stem apex. Thus, the resultant injury does not carry over onto other stem positions and only young leaves are damaged. Agents may prefer different leaves at different times in their lives. *S. albiguttalis* larvae prefer old leaves when they are earlier instars but young leaves as they mature. All of these exceptions to the basic patterns do produce distinct identifiable distributional patterns of their own, however.

Besides spatial-temporal influence on intra-shoot distribution of leaf injury, season plays an important role as does the ability of the plant to outgrow or displace the injury. During the spring or early summer, when leaf production is apt to be most rapid, the injured leaves may be more quickly displaced by new leaves than they would be during the fall or winter. This would tend to restrict the plants to positions lower on the shoot in spring and cause them to appear to "move-up" to higher on the shoot in fall when in fact leaves of equal age are actually being attacked both in spring and fall.

Weevil (*Neochetina* spp.) larvae and adults produce distinctly different
spatial injury patterns on waterhyacinth shoots. Eggs are deposited in the petioles of a middle-aged leaf (third to fourth position) and require up to 2 weeks to hatch. Hence, by the time the first instar larva is present the leaf has moved as much as two positions (to fifth or sixth) depending upon the rate of leaf production. The entire larval period requires 30-45 days and the larvae do not readily move out of the original petiole. Hence, by the time the larvae are mature and large enough to cause significant leaf injury (40 days after oviposition), the plant may have produced five or six leaves and the larva may be in an old (tenth or eleventh position) leaf. Hence, weevil larval injury usually begins to appear in fourth or fifth position leaves and increases on older leaves. A small proportion of mature larvae seem capable of moving into the youngest leaves and this damage is sometimes severe and widespread. In the fall, especially in northern Florida, when leaf production has slowed, weevil larval injury may first appear in younger leaves (e.g. see Figs. 51 and 93).

Weevil adults feed primarily upon the laminae leaving small, squarish lesions and they prefer and seem to concentrate on very young leaves. The most damage is often done to the lamina of the very youngest leaf while it is only partially unfurled. Adults do feed on older leaves also but not to nearly the same extent. As a result, the spatial pattern of adult weevil injury is indistinct increasing only slightly, if at all, on older leaves (e.g. see Fig. 96) but otherwise with a very low or flat slope over leaf positions.

As mentioned above, *S. albiguttalis* larvae feed on old leaves or young leaves. When the plants are tall with erect petioles the older leaves are apparently too hard for the larvae and feeding is restricted to the young, unhardened, first or second position leaves. When the plants are small, early instar larvae feed on the older leaves which usually have soft, spongy, inflated
leaf petioles. In this case, as the larvae mature they often move into and feed upon the young petioles as well. The spatial pattern of injury induced by *S. albiguttalis* larval activity is thus variable depending upon the plant form and the extent of injury. In the former case, especially when the apical bud is destroyed, injury is very high on the first one or two leaf positions and zero thereafter. In the latter case the distribution may be flat, high on young leaves, and increasing on older leaves, or high on old leaves and decreasing on younger leaves (see, for example, Figs. 70, 79, 81, and 105).

The two species of mites produce quite different injury patterns. Spider mites seem to occur in "boom or bust" population cycles. Normally, this species of mite is present in waterhyacinth populations at very low levels. Leaf injury is very sporadic and randomly distributed. Occasionally, outbreaks occur and, when they do, all leaves are affected. The shoots are almost never killed, however, and the outbreaks are generally short lived. As the plants recover the leaf injury is displaced and progressively becomes restricted to older and older leaves.

Waterhyacinth mites were never sufficiently common to discern a recurring pattern. They usually seemed to be restricted to older leaves (see Fig. 52). These are organisms, however, which are restricted to the same leaf through their entire immature period of life and would be vulnerable to displacement on the shoot. Their life cycle from egg to adult requires ca. 3 weeks and a waterhyacinth shoot could produce three or four leaves in that time. Also, injury is usually not conspicuous until later, often not until after the adult emerges from within the leaf. Thus, even if eggs were deposited on the youngest leaves the injury may not be apparent until the leaves are near the fourth or fifth position.
Zonate leaf spot was frequently present at most sites but it, too, was usually restricted to old leaves. Figure 36 shows that at site 2 it was very uncommon on leaf positions younger than fourth or fifth and the same was true at site 4 (Fig. 53). When it was evaluated on the basis of intensity as well as frequency, values were usually too low to be significant and extensive lesions were usually restricted to very old leaves (e.g. see Figs. 69 and 97). This may partially be related to an association with waterhyacinth mite injury but it also may result from antifungal properties of the younger leaves, possibly such as phenol chemistry (Martyn, 1977; Martyn and Freeman, 1978). Also, some data suggest a link between Acremonium infection and increased rates of leaf production (Martyn and Freeman, 1978) which would accelerate displacement of diseased leaves. In addition, the time involved in lesion development following inoculation may be considerable and the leaves may have aged considerably before symptoms appear.

Environmental factors such as frosts or droughts impacted waterhyacinth leaves much like spider mites. They seldom occurred but when they did they affected all leaves. If the plants survived, they eventually were able to produce unaffected new leaves and the injury was displaced.

Other factors such as the pickerelweed borer (Arzama densa) and the pathogen Cercospora spp. were too rare to assess in terms of their spatial distribution on shoots.

Rates of waterhyacinth leaf production varied greatly as is shown in Table 4. High rates generally occurred in flowing systems or in systems with a high nutrient subsidy such as sewage lagoons. The lowest rates occurred when the plants were under stress. Seasonally, leaf production rates are highest in the spring (Center, 1981a). Generally speaking, the slower the plants are able to
regenerate damaged leaves, the greater the impact of natural enemies.

Waterhyacinth seem to be adapted to withstand leaf injury by rapidly regenerating leaves and by sloughing injured leaves. The impact of any stress factor on a waterhyacinth shoot is dependent upon the rate at which a shoot can replace a damaged leaf relative to the time it takes that stress factor to fully develop. Organisms which feed upon or infect the leaves, then, are faced with the problem of being able to persist on the plant. Thus, either their life cycle must be in phase with the leaf's life cycle or they must be able to move to new leaves or other parts of the plants when the leaf dies. The various agents have apparently solved this problem in different ways. But, for biological control to be effective, the defensive strategy of the plant must be overcome. Only S. albiguttalis and the two weevil species seem able to consistently do this.
Table 4. A comparison of average rates of waterhyacinth leaf production per shoot among various sites.

<table>
<thead>
<tr>
<th>Site No.</th>
<th>Site</th>
<th>Dates</th>
<th>Leaf Production Rate (leaves per day)</th>
<th>Rank</th>
</tr>
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<tbody>
<tr>
<td>4</td>
<td>Lake Alice</td>
<td>10 MAR - 7 OCT '81</td>
<td>0.126</td>
<td>5</td>
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<td>6B</td>
<td>Oxy</td>
<td>SEP - NOV '80</td>
<td>0.097</td>
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<td>Oxy</td>
<td>MAY - OCT '81</td>
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<td>0.035</td>
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<tr>
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<td>Lake Okeechobee</td>
<td>18 JAN - 19 JUL '82</td>
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REFERENCES CITED


Knipling, E.B., S.H. West, and W.T. Haller. 1970. Growth characteristics,


