Biological Control of Aquatic and Wetland Weeds in the Southeastern United States

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Abstract

Exotic weeds of aquatic and wetland habitats restrict irrigation, flood control, mosquito control, navigation and recreation, and threaten native plant communities throughout the southeastern United States. Traditional control relies on chemical or mechanical methods but biological control is increasingly important. Past biological control projects on alligatorweed (Alternanthera philoxeroides) and waterhyacinth (Eichhornia crassipes) were quite successful. Alligatorweed is no longer a major weed in coastal regions and waterhyacinth infestations have been reduced. This is well-documented in Louisiana, where waterhyacinth acreage has declined from 1.2 to < 0.4 million acres. Projects are now underway on waterlettuce (Pistia stratiotes), hydriella (Hydriella verticillata), and melaleuca (Melaleuca quinquenervia). An ephryd fly (Hydrellia pukaniaca) and a weevil (Bagoos affinis) were released on hydriella in 1987. A second fly (Hyperlae weevil (Bagoos affinis) sp.) and another weevil (Bagoos affinis sp.) are being studied in U.S. quarantine. Three aquatic pyralid moths (Nymphula eponenta, Astacodes siennata, and Streptosoma reptialis) will be evaluated in Australia. Neohyadronous psilochilus, a weevil used successfully against waterlettuce in Australia, was released during 1987 and is established at five sites. A noctuid moth (Namanga psilochilus) used for control of waterlettuce in Thailand is being studied in U.S. quarantine. Faunal inventories of melaleuca have recently begun in Australia and several potentially useful candidates have been found.

Introduction

Aquatic weeds are not unique to the southeastern U.S.A., but a combination of factors have created notorioussly severe infestations there. The warm climate and prolonged growing season of the area promotes luxuriant plant growth. Warm, shallow, often naturally fertile aquatic systems foster proliferation of invasive aquatic species. Agricultural land use exacerbates problems by providing nutrient-rich run-off from pastures and fields that flows into surrounding aquatic systems. Perhaps the greatest single cause of aquatic weed problems is the prevalent public attitude that tolerates the importation of exotic plant species for decoration of aquaria or ponds. This has encouraged the deliberate introduction of several invasive species. Those that are of the most immediate concern in the southeastern U.S.A. are waterhyacinth (Eichhornia crassipes Martius (Solms-Laubach); Pontederiaceae), waterlettuce (Pistia stratiotes L.; Araceae), hydriella (Hydriella verticillata [L.f.] Royle; Hydrocharitaceae), Eurasian watermilfoil (Myriophyllum spicatum L.; Haloragaceae), alligatorweed (Alternanthera philoxeroides (Martius) Grisebach; Amaranthaceae), and paperbark tree (Melaleuca quinquenervia Cav.) (Blake; Myrtaceae).

The quest for biological controls of aquatic weeds began in 1960. Alligatorweed, being difficult to control by other means, was assigned top priority. A USDA scientist, backed by funding from the U.S. Army Corps of Engineers, surveyed for natural enemies in South America during 1960-2. A scientist from Uruguay then studied natural enemies of waterhyacinth between 1962-3. A USDA/ARS laboratory was established near Buenos Aires, Argentina, in 1962 to evaluate further the insects discovered earlier. This research was conducted by D. M. Maddox from 1962-7, B. D. Perkins from 1968-71, and C. J. DeLoach from 1971-4.

Other limited aquatic weed projects were initiated that were somewhat opportunistic in nature. For example, a project implemented in cooperation with the CIBC Pakistan Station
commissioned surveys for natural enemies of hydrilla during 1971-6. Yugoslavia was surveyed for natural enemies of Eurasian watermilfoil under a cooperative arrangement with the Yugoslavia Plant Protection Institute during 1967-9. Although Pemberton (1980) surveyed briefly in Africa for natural enemies of hydrilla during 1976, foreign exploration and evaluation of candidate biological control agents essentially ceased after DeLoach left Argentina in 1974. The last biological control agent to result from these early projects was released in 1977.

The limited scope of the early surveys of submerged aquatic weeds restricted their usefulness. Considerations other than scientific principles (center of diversity, ecoclimatic criteria, origin of the noxious form, etc.) dictated the regions chosen for surveys. Traditional scientific rationale were difficult to apply to either hydrilla or Eurasian watermilfoil, so surveys of their entire native ranges were deemed necessary (Wapshere 1981).

Although interest in biological control is increasing, the importance of foreign studies is largely unappreciated. In 1981, the future of the aquatic weed program in the U.S.A. appeared grim. No new biological control agents had been released in 4 yrs (only six in the 20-yr history of the program) and, because of the lack of exploration, no prospects for future releases were in sight.

Fortunately, the U.S. Army Corps of Engineers considered biological control to be an important component of their Aquatic Plant Control Research Program. They provided sufficient funding for limited foreign surveys on hydrilla. These funds supported comprehensive surveys by CIBC in East Africa during 1981-4. They also enabled one of us (JKB) to devote 15 months to exploration within the Indo-Pacific range of hydrilla during 1981-3. Many insects that would feed on hydrilla were found, but most were undescribed species or unidentifiable specimens. As a bonus, successful biological control of waterlettuce observed in Thailand and Australia provided the impetus for initiation of a similar project in the U.S.A. These foreign studies rejuvenated the aquatic weed program and we are optimistic about its future.

Much progress has been made in the aquatic program since 1981. Successful biological control of waterhyacinth has been corroborated. Insects have been introduced for the first time for control of a submerged weed. Waterlettuce and paperbark tree have been targeted for biological control and new projects have been initiated. In this paper we provide current information on waterhyacinth, hydrilla, waterlettuce, and paperbark tree. These projects represent unusually close cooperation among several agencies, particularly the U.S. Army Engineers (USAE), the USDA Agricultural Research Service (ARS), the University of Florida (UF), and the National Park Service (NPS). We have drawn heavily upon the work of Dr. Gary Buckingham (USDA) and Dr. Dale Habeck (UF) for discussions of progress reported herein.

Waterhyacinth

History

Waterhyacinth is a large, floating aquatic macrophyte that is native to the New World tropics. It was imported to the U.S.A. in 1884 for display at the New Orleans Cotton Exposition. Exhibitors purportedly provided live specimens to visitors. The inevitable happened, and progeny of these specimens wound up in natural aquatic systems. The plant’s range expanded rapidly, and by 1888 it infested coastal fresh waters of Texas, Louisiana, Mississippi, and Alabama. It reached Florida in 1890, Georgia in 1902, and California by 1904. Introductions occurred almost simultaneously in the late 19th and early 20th centuries throughout the Old World tropics. It now occurs worldwide mainly in tropical and subtropical regions but reaches latitudes of 40°N (Portugal) and 40°S (New Zealand).

Emphasis on biological control of waterhyacinth was delayed until after completion of the alligatorweed project. Three insect species were released ultimately on waterhyacinth. Two were weevils, Neochetina eichborniae Warner and N. bruchi Hustache (Coleoptera:
Curculionidae), released in Florida in 1972 and 1974, respectively. The third is a moth, *Sameodes albiguattalis* Warren (Lepidoptera: Pyralidae), released in Florida in late 1977. DeLoach (1975) rated each candidate using Harris' (1973) rating system and ranked *S. albiguattalis* more highly than either species of weevil.

**Impact of Biological Control Agents**

Several published studies demonstrated the potential for biological control agents to impact waterhyacinth populations under controlled conditions (Forno 1981, Center et al. 1982, Del Fosse et al. 1976a, DeLoach and Cordo 1976, Bashir et al. 1984, Goyer and Stark 1981, 1984). Field studies in the U.S.A. further showed the decline of waterhyacinth at many sites after introductions of biological control agents (e.g., Center and Durden 1986, Center 1987, Goyer and Stark 1981, 1984, Cofrancesco 1985, Cofrancesco et al. 1985). Other countries then imported these biological control agents (Julien 1982). Successful biological control of waterhyacinth has been reported in Australia (Wright 1979, 1981), Argentina (DeLoach and Cordo 1983), India (Jayanth 1987), and the Sudan (Girling 1983, Beshir and Bennett 1985).

**Impacts at Florida Sites**

We have observed two distinct patterns of declines in waterhyacinth populations in Florida. Examples are provided from Lake Alice in north Florida and Canal-M in south Florida. In the first case, the waterhyacinth population was slowly replaced by other floating species. In the second case, the entire waterhyacinth population dropped out relatively rapidly.

Lake Alice is a 80 acre lake on the University of Florida campus of which about two-thirds is a shallow marsh (Center and Spencer 1981). In the early 1970s, the waterhyacinth in this marsh comprised a monoculture covering approximately 50 acres. During summers the waterhyacinth population regularly expanded into the open lake area when as much as 79% of the 80 acre system became infested. *N. eichhorniae* readily established in the marsh after its release in 1974. Populations increased slowly and peaked 4 yrs later (Fig. 1). As weevil populations increased, plant size correspondingly decreased. The population density of ramets thinned. Other species, such as *Hydrocotyle* spp. (Umbelliferae) (formerly predominant only during spring) persisted throughout the year (Fig. 1). This was associated with slower early season growth of waterhyacinth (Fig. 2) and later attainment of maximal biomass. By 1982 waterhyacinth infested only about 5% of the lake.

Adult weevil populations seemed low during spring, but ecological density showed a different pattern. Larval intensity (galleries per unit mass of leaf tissue) typically peaked in May. Adult intensity (number per unit of biomass) typically peaked twice during the year, once during February to April and again during August to October. These early intensity peaks altered the phenology and competitive relationships within the floating community so that waterhyacinth was gradually replaced by *Hydrocotyle* spp. as the predominant mat-forming species. The dense *Hydrocotyle* mat with its tightly interwoven stems trapped detritus within the interstices and formed a peat-like mud. This in turn provided a substrate in which emergent species established. The replacement of waterhyacinth then initiated a successional pattern of changes in community composition that resulted in a diverse floating community. Curiously, even though waterhyacinth persisted as a component of this community, it never again expanded outward from the marsh into the open lake. The university suspended waterhyacinth control operations in the lake after 1977.

At Canal-M, we studied an area where a waterhyacinth infestation had been removed by herbicide application, but where a fringe of plants had regrown. We tagged several plants within this fringe in December 1981 to determine the fate of individual ramets. *S. albiguattalis* heavily infested these small plants and soon killed 31% of the tagged ramets. *S. albiguattalis* did not persist after April when plants extended across the canal, the surface closed over, and plant morphology shifted to the tall form. Both *N. eichhorniae* and *N. bruchi* then became more abundant. They eventually killed another 43% of the tagged plants. By the end of 1982 these weevils also killed about 33% of a second group that we tagged in May. By then, *N. bruchi* was no longer present and all plant mortality was attributable to *N.
*Eichhornia*. This study demonstrated the importance of all three insect species; the resulting papers (Center and Durden 1986, Center 1987) should be consulted for more details.

Leaf production dynamics were also studied on these tagged plants. We found that even when biological control agents didn't kill the plants, their impacts were important. Specifically, biological control agent infestations induced leaves to die slightly faster than the plants could produce them. This imbalance caused a net loss of about one leaf every 100 d. Waterhyacinth, like plants such as palms, requires a minimal leaf complement. A mature ramet normally bears six to eight leaves, but at Canal-M, this number gradually dwindled (Center 1987). The plants then slowly lost buoyancy and sank. Even though this demise was attributable to the insects, little direct evidence would have connected the two events if we had not monitored the fate of individual leaves.

![Graph showing leaf length, plant biomass, and weevil population over time](image)

**Figure 1.** Data from Lake Alice. The top graph shows the gradual increase in numbers of adult *Neochetina eichhorniae* Warner per ramet, the reduction of plant size, and the change in plant phenology as peak plant size shifted from early to late summer. The bottom graph shows the increased representation of other plant species (mainly *Hydrocotyle* spp.) in the floating community as waterhyacinth decreased.

**Impacts in Louisiana**

Information from Louisiana provides the best-documented example of a regional impact by waterhyacinth biological control agents. The Louisiana Department of Wildlife and Fisheries (LDWF) conducts semiannual (spring and fall) surveys in nine regions (Fig. 3) on the extent of waterhyacinth infestations. The major infestations occur in the Atchafalaya Floodway Basin (Region 3) and the Port Allen Intracoastal Waterway (Region 2).

*N. eichhorniae* was first released in 1974 at a few sites (Manning 1979). By 1976 weevils had been released throughout Louisiana and populations were well-established by 1978. *N. bruchi* was released in 1975 and *S. albipustulatus* was released in 1980.
In 1974, fall surveys showed approximately 1.06 million acres of waterhyacinth in Louisiana (Fig. 4). In 1975 this increased to 1.72 million acres, but the increase was attributable to an unusually wet winter, spring, and summer. Habitat availability increased so the waterhyacinth populations expanded. Later years were more typical with 1.10, 1.18 and 1.07 million acres in 1976, 1977, and 1978, respectively. The fall average for this initial 5-yr period was 1.23 million acres. The spring average was 608,000 acres, so annual growth averaged about 620,000 acres.

![Graph showing standing crop from 1974 to 1980](image)

**Figure 2.** Data from Lake Alice showing changes in waterhyacinth phenology over a seven-year period for the months of April, June, and October. Peak yield was reduced and shifted from early to late in the growing season. The spring flush of growth that occurred 1974-6 was suppressed after 1976.

Biological control agent populations were low and had no impact on acreages during the initial 5 yrs. The weevils (particularly *N. eichhorniae*) first began to impact sites by 1979. Also, at this time fall acreage was unusually low (855,000 acres). By 1980 widespread waterhyacinth decline was evident, and fall estimates dropped to 301,000 acres. Extremely large *N. eichhorniae* populations accompanied this decline. We observed millions of weevils flying and accumulating at lights during August. We presumed this to be a dispersive response stimulated by deteriorating plant quality.

Waterhyacinth acreage has remained low since 1980. Fall estimates for the 5-yr period of 1981-5 averaged 357,834 acres and ranged from 208,300 acres (1985) to 567,650 acres (1983). Spring acreages during the same period averaged 196,576 acres with a range of 103,300 to 365,400 acres. Average annual growth then was only 161,258 acres. Comparison of the two 5-yr periods shows that fall acreage declined by 71%, spring acreage by 68%, and annual growth by 74%. Lowered spring acreages alone failed to account for fall reductions, since data for 1977-9 proved waterhyacinth capable of rebounding to high levels following severe winter diebacks. The impact of the biological control agents was manifested as reduced productivity over the growing season rather than an induced dieback, although both probably occurred.
Figure 3. A map of Louisiana showing the nine regions surveyed semiannually by the Louisiana Department of Fisheries and Wildlife to assess the extent of waterhyacinth infestations.

We contend that the reduction in waterhyacinth acreage directly resulted from the introduction of biological control agents, specifically \textit{N. eichhorniae}. Skeptics refute this contention. They have suggested that one of four other factors could have accounted for the waterhyacinth decline in Louisiana. These are: (1) herbicide treatments; (2) temperature extremes; (3) salt water intrusion; or (4) change in patterns of precipitation.

\textit{The herbicide hypothesis.} This hypothesis is easily disputed since herbicides can only be applied to a relatively small proportion of the total infested area. Cost and accessibility limit the number of acres that can be treated. From 1978-85, no more than 80,000 acres were treated with herbicide during any 1-yr period. In many instances the same areas were retreated multiple times, so the total acreage actually treated was probably < 40,000 acres. Even assuming that 80,000 acres were removed with no regrowth, this would account for only a fraction of the total reduction.

\textit{The temperature hypothesis.} Being a tropical plant, the occurrence of unusually cold periods could explain a temporary decline in the statewide acreage of waterhyacinth. The existence of a cooling trend would be necessary to explain the documented long term decline. Temperature data from New Orleans, Baton Rouge, and Lake Charles (Fig. 5) show no
persistent shift towards colder winters. One of the coldest winters on record occurred during 1976-7. The following spring acreage decreased to only 217,400 acres yet it increased to over 1 million acres during the following growing season. Later declines to similar levels during the 1981-5 period failed to rebound. Suppression of fall acreage was due to reduced seasonal growth, not to reduced initial stock. This fact alone refutes the temperature hypothesis.

**TOTAL WATERHYACINTH ACREAGE IN LOUISIANA**

![Graph showing total waterhyacinth acreage in Louisiana from 1974 to 1985.](image)

Figure 4. Estimates of fall and spring waterhyacinth acreages for the state of Louisiana for the 11-yr period following the release of *Neochetina eichhorniae* Warner.

*The precipitation and salt water intrusion hypotheses.* These two hypotheses are obviously interrelated and must be dealt with together. Reduced precipitation could be conducive to salt water intrusion. Extremely high precipitation levels could cause an increase in waterhyacinth acreage such as that experienced during 1975. Precipitation records are provided for Baton Rouge, New Orleans, and Lake Charles in Fig. 6. These data show no long-term changes consistent with the observed changes in waterhyacinth acreages. Periods of high rainfall and periods of drought occurred often, but were relatively evenly distributed over the 11-yr period.

Salt water intrusion effects would be most evident in coastal areas, particularly in the Port Allen area. It would be least evident in the Atchafalaya Basin, which is protected by an intrusion barrier at Morgan City. If waterhyacinth declined in the Port Allen area but not in the Atchafalaya Basin, then the intrusion hypothesis would seem plausible. Such was not the case. Figure 7 shows similar patterns of decline in both areas. We therefore reject the salt water intrusion hypothesis.
Figure 5. National Oceanic and Atmospheric Administration records for average temperature at Baton Rouge, Lake Charles and New Orleans, 1974-85.
The biological control hypothesis. Any careful observer visiting sites in Louisiana during the early 1980s would have no difficulty in selecting this as the correct hypothesis. Huge *N. eichhornia* populations caused extensive and obvious plant damage. The massive dispersal flights of weevils in August 1980 (Center 1982) and again in September 1983 (Buckingham, pers. comm.) attest to their abundance. Individual sites monitored during this period were severely impacted by the weevils. Examples include Lake Theriot (Fig. 8) and the Assumption Parish sites (Cofrancesco et al. 1985) as well as sites at Morgan City and Whitehall (Goyer and Stark 1981, 1984). Biological control is the only logical hypothesis available to explain this massive decrease in waterhyacinth acreage that is supported by data.

Figure 6. National Oceanic and Atmospheric Administration records for monthly precipitation totals at Baton Rouge, Lake Charles and New Orleans, 1974-85.

Impacts in Texas

Waterhyacinth occurs mainly in the southeastern portion of Texas. No figures on the extent of the infestation are available, but specific sites have been monitored since 1980.
N. bruchi was released in Texas at Wallisville Reservoir 1980. N. eichhorniae populations, that presumably immigrated from Louisiana, were found in Texas in 1980 at the J.D. Murphy Wildlife Area. This species later was found at Wallisville Reservoir in 1982. Figure 9 shows increasing adult weevil populations over successive years at Wallisville Reservoir. The waterhyacinth mat entirely dropped out (Fig. 10) due to heavy damage associated with a substantial increase in the weevil populations in 1983.

Figure 7. Spring and fall waterhyacinth acreages in the Port Allen region (top), the area most likely to be influenced by salt water intrusion, and the Atchafalaya Basin (bottom), which is protected from salt water by an intrusion barrier at Morgan City.
Impacts in the Sudan

The work in the Sudan has been particularly interesting because of the dramatic impact documented by Dr. Beshir (Beshir and Bennett 1985). The Sudanese government has had an intensive, ongoing waterhyacinth control campaign for many years. This effort focused on

Figure 8. Lake Theriot in Louisiana before (top photograph; June 1979) and after (bottom photograph; July 1982) the effects of Neochetina eichhorniae Warner caused a decline in the plant population. This canal was blocked at both ends thus eliminating the possibility that the plants drifted away.
preventing the spread of waterhyacinth from upstream reaches of the White Nile to below the Jebel Aulia Dam. The program cost in excess of one million Sudanese pounds annually, and relied upon chemical control. Release of biological control agents began in 1978 with *N. eichhorniae*. It established readily and occurred throughout a 1700 km stretch of the White Nile system by 1981. *N. bruchi* was established by 1981 and *S. albivittalis* was widely established by 1983. The impact of these insects was astounding. No accumulation of waterhyacinth occurred behind the Jebel Aulia Dam between 1982-84 according to Beshir and Bennett (1985). They, in fact, reported the plant to be scarce a distance of 30 km upstream from the dam. In contrast, large masses of plants (up to 11,350 ha) had accumulated at the dam every year since the early 1960s (waterhyacinth was introduced in the mid-1950s), and maintenance previously required constant vigilance and frequent herbicide treatments.

**Neochetina ADULTS**  
**WALLISVILLE, TEXAS**

![Graph showing the growth of Neochetina adults](image)

Figure 9. Growth of the population of waterhyacinth weevil adults (means per plant ± 2 SE) at Wallisville Reservoir in Texas during the 4 yrs following their release.

**Hydrilla**

**History**

Hydrilla is a submersed, caulescent vascular hydrophyte that is widely distributed in the Old World. Cook and Luond (1982) suggested that its center of origin lies in tropical Asia. Its
distribution extends almost continuously from Iran and Afghanistan through Pakistan, India, and Southeast Asia, then extends northward along coastal China to the Soviet Union, Japan and Korea, and southward through the Indo-Pacific region to coastal regions of Australia. Several disjunctions in this range occur. It exists naturally in Africa only in and around the central African Rift Valley lakes. A discrete population occurs in northeastern Europe.
(Poland and Lithuania), and an extirpated population existed until ca. 1945 at Esthwaite Water in England. A small population still survives in Ireland (Cook and Luond 1982).

Numerous extralimital introductions of hydriella have apparently taken place, for Cook and Luond (1982) indicated that populations in Mozambique, the Ivory Coast, the Canary Isles, New Zealand, Austria, the U.S.A., Panama and Jamaica were recently introduced. Pieterse (1981) suggested that it was probably also introduced to Fiji, and Swarbrick et al. (1982) considered it adventive on Mauritius. Curiously, severe, problematic infestations have resulted only from the introductions into New World localities.

The first New World introduction was in Florida, probably around 1960 (Blackburn 1969). It rapidly dispersed. By 1967 it was a serious weed throughout central and south Florida and was found at Lake Seminole on the Florida-Georgia border (Haller 1978). It first spread to neighboring States in the Southeast and was recorded in Louisiana in 1973 (Wherry 1974), Texas in 1974 (Guerra 1976), Iowa in 1972 (Cook and Luond 1982), and California by 1976 (Sonder 1979). Steward et al. (1984) reported the occurrence of a new monocious biotype from the Potomac River near Washington, D.C., during 1982. Hydriella was present in North Carolina during 1979 (Langeland and Schiller 1983) and in Delaware in 1981 (Haller 1982). Since then it has continued to expand and new records of its occurrence anywhere in North America would not be unexpected.

Faunal Inventories

As noted earlier, usual scientific rationale that govern the choice of geographic areas in which to search for biological control agents were difficult to apply in the case of hydriella. Determination of the geographic center of diversity is one criterion listed by Wapshere (1981). But the genus is monotypic, so no center of diversity exists. The Hydrocharitaceae is a cosmopolitan family composed of 15 genera, and all species are aquatic or marine (Cook et al. 1974). The distribution of the family also provides no clear biogeographical clue to the origin of the group in general nor to the origin of hydriella in particular.

Wapshere (1981) also suggested that agents be chosen from regions within the plant’s native range that are ecologically analogous to the area where the weed occurs at noxious levels. This focuses the search on biological control agents that are preadapted to the climate in the region where they are to be released. Hydriella is native mainly to the Old World tropics, but is a noxious weed in subtropical and temperate parts of North America. Comparable climates occur within its native range only in temperature Asia and Australia. Political considerations limited our ability to survey in China and we thought that the weed was adventive in Australia.

A third criterion involves identifying the origin of the noxious form of the weed, and then searching within that area for effective biological control agents (Wapshere 1981). In doing so, the biological control agents found would be preadapted to the noxious strain. The origin of the U.S.A. strains of hydriella are uncertain. Haller (1978) stated that it was first introduced to Florida from South America, but South America is not with the native or adventive range of hydriella. Stanley and Gangstad (1977) speculated that hydriella was introduced from Southeast Asia. Others suggested that Africa was the area of origin (Sonder 1979, Mahler 1979). Cook and Luond (1982) list chromosome counts from various areas of the world that show hydriella as diploid (2n = 16) or triploid (2n = 24) within its native range, but material from the U.S.A. (Alabama) as tetraploid (2n = 32). All U.S.A. populations examined by Verkleij et al. (1983), however, were triploid, with exception of the strain from Washington, D.C. This one constituted a distinct diploid monocious strain (Steward et al. 1984). Other U.S.A. strains are dioecious and only bear female flowers. Ploidy level seems irrelevant to the origin of the plant because diploids and triploids are sympatric in many parts of the world (Cook and Luond 1982). Verkleij et al. (1983) found a tremendous statistical overlap in morphology among biotypes based on characteristics measured on plants grown under identical conditions. They concluded from chromosome numbers, isoenzyme patterns, and morphology that the origin of the predominant North American biotype was uncertain. Pieterse et al. (1983) later compared African plants with plants from other areas. Isonzyme patterns of African hydriella most closely resembled the U.S.A. strain from Gulf coastal States.
and California, a strain from Kashmir, and strain from Indonesia. However, morphology of the African specimens readily separated them from the other biotypes. Pieterse et al. (1985) concluded that an African origin of U.S.A. plants was unlikely because of differences in chromosome numbers.

We concluded that available information was inadequate to accurately preselect a single geographical area in which to survey. We therefore elected to conduct random surveys (sensu Wapshere 1981) throughout the native range of the plant to assess directly the richness of potential biological control agents. The information acquired would be used to determine the areas with the greatest diversity of organisms that feed on the plant. As a prelude to this, we surveyed in the U.S.A. to inventory the herbivorous species present on hydridilla (Balciunas 1984, Balciunas and Minno 1985). This served two purposes. First, it demonstrated the depauperate nature of the herbivorous fauna in the U.S.A. Second, it enabled us to exclude from later consideration those species shared between U.S.A. and foreign faunas.

A few earlier projects had provided information on potential biological agents of hydrilla. Thorou: studies done in Pakistan by CIBC 1971-6 identified ten species of potential biological control agents (Baloch et al. 1980, Baloch and Sana-Ullah 1974). Three general groups of insects attacked hydrilla: aquatic nymphuline moths; bagoine weevils; and ephryid flies.

In 1977, Pemberton (1980) conducted a brief three-month survey in Africa. After two months of searching he finally came upon hydridilla in Lake Tanganyika. He found no representatives of the above-mentioned groups. However, he found midge larvae, ostensibly in the genus *Polypedilum* (Diptera: Chironomidae), that appeared to burrow into stem apices. These larvae destroyed the apices of 65 to 80% of the stems examined. The resultant damage caused the plants to become multi-branched and stunted. Pemberton (1980) speculated that this, in association with tip pruning by herbivorous fish, prevented the plant from becoming a problem in Lake Tanganyika. He also found a mayfly (*Povilla adusta*; Ephemeroptera) that burrowed within hydridilla stems.

Markham (1986) followed up on Pemberton’s base-line studies during 1981-4. He surveyed extensively in Kenya in the hopes of finding a source of hydridilla that was near the CIBC laboratory in Muguga. Herbarium records showed a historical distribution of hydridilla in Kenya, particularly at Lake Victoria, but exhaustive searches failed to uncover it. The plant apparently has been extirpated from much of its former African range. Markham (1986) managed to find hydridilla at Lake Kioga in Uganda, at Lake Bulera and the Mukungawa River in Rwanda, and at Lake Tanganyika in Burundi. He confirmed the damage done to hydridilla by midge larvae, and successfully reared them on hydridilla, thus proving their association with the plant. Aquatic pyralid larvae on hydridilla in the Mukungawa River didn’t cause extensive damage and were non-specific.

Varghese and Singh (1976) conducted limited searches for insects on hydridilla in Malaysia during 1973-6. They found only two potentially-useful species, an aphid, and a nymphuline moth. The aphid was not specific and the moth was probably *Parapoxyn diminutalis* (Snellen) (Lepidoptera: Pyralidae), a species accidentally introduced into the U.S.A. (Del Fosse et al. 1976b).

Aquatic weed control specialists from the U.S. Army Corps of Engineers observed damage to hydridilla in the Panama Canal during summer 1978. The damage was caused by aquatic moth larvae, and specimens of adults were collected. These were identified as *Parapoxyn rugosalis* (Moschler). We travelled to Panama during May 1979, and encountered an aquatic moth that was severely-impacting hydridilla mats. We conducted preliminary host-specificity tests, and concluded that larvae were specific to caulescent-stemmed species of aquatic plants (Balciunas and Center 1981). Specimens sent to Dr. Eugene Munroe were identified as a new species of *Parapoxyn* but not *P. rugosalis*. Later, Buckingham and Bennett (1984) obtained insects from the same area. Curiously, these proved to be neither *P. rugosalis* nor *Parapoxyn* n.sp., but rather *P. diminutalis*, the Asian species earlier found in Florida.

In 1981, we began to search for potential biological control agents throughout the Indo-Pacific range of hydridilla (Balciunas 1985). This foreign exploration occupied about 15
months during 1981-3. Brief surveys were conducted in parts of India, Sri Lanka, Burma, Thailand, Malaysia, Indonesia, the Philippines, Australia and New Guinea. This strategy was based upon the assertion that most potential biological control agents are found early in the exploration phases. If true, it should be more productive to briefly survey over a broad range rather than to thoroughly survey in a few places. During these trips about 45 species of insects that would feed when presented with hydrilla were found (most were undescribed species so an exact tally is impossible). Additionally, species earlier studied in Pakistan were discovered in other places, and their status as potential biological control agents was upgraded. Most of the species found were either nymphauline moths (ca. 18 species), ephydrid flies (4 to 6 species), or bagoine weevils (5 species collected from hydrilla, plus 23 species that would feed when provided with hydrilla), the same groups studied in Pakistan. Other groups, such as chironomid larvae and trichopteran larvae, were found but were not ranked highly among candidate agents.

First Releases of Hydrilla Biological Control Agents

During these surveys, some of the insects originally listed as promising candidates in Pakistan were found in India. Field observations reaffirmed their candidacy and two species were referred to U.S.A. quarantine. These were a bagoine weevil, Bagous affinis Hustache (Coleoptera: Curculionidae) and a fly Hydrelia pakistaniæ Deonier (Diptera: Ephydridae). Both species were proven to be host-specific by Dr. G. Buckingham and were approved for release.

B. affinis is, unfortunately, not aquatic although adults will feed on hydrilla at the water surface. Larvae feed on the subterranean hibernacula (tubers) but only in dry soil. Females oviposit on moist, rotting wood near the edge of a receding water body. Larvae burrow through the dry soil until they encounter a hydrilla hibernaculum, then burrow into and destroy it. Because these hibernacula enable the plant to survive unfavorable periods (e.g., drought, herbicide exposure), their destruction could enhance other control measures.

These weevils will be most useful where water levels can be manipulated. We envisioned their implementation in conjunction with lake or canal drawdowns, especially in arid areas such as southern California where irrigation canals can be dewatered. Plans are presently being made for the release of B. affinis in that area. Meanwhile, the first release of about 1200 adults was made 30 April 1987 at Lake Tohopekaliga in central Florida. This lake had been partially drawn down to expose a wide swath of shoreline. Additional releases have been made in Florida in wetter habitats, but no effort has been made to determine if populations have established.

H. pakistaniæ was released on 29 October 1987 at Lake Patrick in Polk County, Florida. Subsequent releases were made at south Florida sites. Adults were recovered from Lake Patrick in February 1987, and from Everglades Holiday Park (Broward County) in April. Baloch et al. (1980) and Baloch and Sana-Ullah (1974) describe the life history of this fly. Adult females lay eggs on floating substrates. Larvae descend into the water column until they encounter hydrilla. They mine the leaves to feed on the mesophyll. A single larva during its 9 to 16 d development can destroy a dozen leaves. The life cycle requires about 4 wks and each female lays up to 38 eggs.

Australian Studies

Wapshere (1974) noted that when a decision on a search area is based upon non-biological factors such as personal convenience, availability of laboratories, etc., then the searches are unlikely to be of great value. Yet, these factors were prime considerations in our selection of Australia for more intensive field surveys. Funding for this work was minimal, and Australia seemed to be the location where the most could be accomplished with limited resources. However, some biological factors supported this choice. Contrary to our early information, hydrilla is native to Australia (Cook and Luond 1982, Swarbrick et al. 1982). The range of hydrilla in Australia encompasses ecoclimatic zones that resemble areas in the U.S.A. where it is particularly noxious. Also, the three predominant groups of potential biological control
agents associated with hydrilla were all present. Therefore, in cooperation with CSIRO and later with James Cook University, we established a field station at Townsville in northern Queensland in January 1985. Studies on Australian hydrilla insects will continue until mid-1989.

This work focuses upon the evident specificity of selected species, based upon field observations and collections of various aquatic plant species. Laboratory studies support field data and provide data on the bionomics of candidate species. The Australian species of greatest interest to us is a bagoine weevil. It was first identified as Bagous australiastiae Blackburn, but is now considered a new species in the same genus. Larvae and adults feed on the plant and cause extensive damage. The adult weevils lay eggs in hydrilla stems and larvae burrow within the stems. This, accompanied by damage from the adults, causes the shoots to fragment and float to shore. The larvae then pupate in the soil near the strand line or in stranded material. Larvae feed and complete development in the laboratory on related Hydrocharitaceae, but they rarely do so in the field. This species has now been imported to U.S.A. quarantine.

A second Australian species of interest is a fly that was originally identified as Hydrellia unigena Cresson (Diptera: Ephydridae). This also is now considered to be a new species. Although this species was sometimes found in collections of other aquatic plants, over 97% of the specimens were collected from hydrilla. Therefore, it too was referred to U.S.A. quarantine where it is now being evaluated.

Two species of nymphaline aquatic moths were found attacking hydrilla in Australia early in this project. The first was Nymphula dicentra Meyrick, which is similar to, and perhaps conspecific with, P. diminutalis. The second was Nymphula eromenalis Snellen. Larvae of both species were found feeding on other plants and seemed to lack host-specificity. However, the larvae thought to be N. eromenalis were reared to adults and found to actually represent a species, N. eromenalis, Aulacodes siennata Warren, and Strepstinoma repitillus (Walker). This cast previous presumptions of host-specificity in doubt. Later studies indicated that one of these species, A. siennata, preferred hydrilla. This is a stream-dwelling species from northern Australia that has thus far been difficult to rear and study under laboratory conditions. Determination of host-specificity of this is our top priority for continuation of the Australian studies.

Paperbark Tree

History

The paperbark tree (M. quinquervia) is a medium-to-large Australian tree that usurps wetland habitats in the U.S.A. During the evolution of the genus, Melaleuca emigrated northward from the tropical mainland of Australia. Thus, a few species are included as elements of extra-Australian floras (Debeneham 1963). Otherwise, the genus is wholly Australian in distribution and its origin is clearly in tropical Australia. Approximately 250 species occur throughout Australia (Barlow 1986). Eleven species closely allied with M. quinquervia comprise the M. leucadendra complex (Blake 1968). The center of diversity for this complex is clearly defined in northern Queensland, particularly in the area of the Cape York peninsula.


In Florida, M. quinquervia exists mainly in the south, below Lake Okeechobee. Major infestations occur along the southern edge of Lake Okeechobee, along the eastern edges of Dade, Broward, and Palm Beach Counties to the east, and within the western half of Lee County to the west (Capchert et al. 1977). A significant infestation also occurs in southeastern Collier County in the Big Cypress area. Records of individual trees have been reported from as far north as Gainesville in Alachua County (latitude 30°N) (Pritchard 1976).
Dr. H. Nehrling introduced *M. quinqueloria* into Florida in 1900 by planting seeds near Orlando (Meskimen 1962). Pritchard (1976) states that J.C. Lang also introduced the plant at about the same time. A professor of Tropical Forestry at the University of Miami, Dr. J.C. Gifford, probably first established the species in south Florida. He received seeds in 1906 from Sydney and planted seedlings along Biscayne Bay.

Specimens or seeds were later given to F. Stirling, a nurseryman from Davie in Broward County (Meskimen 1962, Gifford 1937).

In 1912, A.H. Andrews introduced the plant to the west coast of Florida at Estero in Lee County (Meskimen 1962, Pritchard 1976). This introduction accounts for infestations on the lower Gulf coast.

In 1936, H. Stirling collected seeds from Davie and spread them by airplane in the eastern Everglades (Meskiman 1962). Further spread was caused by nurserymen who transplanted saplings from the Gulf coast and propagated them as landscape plants. The populations south of Lake Okeechobee were started in 1941, when trees were planted on levees and spoil islands for erosion control (Stocker and Sanders 1981, Greene 1983). By 1980 nearly 460,000 acres or 6% of the total land area of south Florida contained paperbark infestations. Marshes comprised over half of the infested acreage (250,604 acres) and 13% of all marshlands in south Florida contained infestations (Cost and Carver 1981).

Impact of Melaleuca Infestations

Because of the type of habitat it occupies, *M. quinqueloria* impacts environmentally-sensitive areas. These include Everglades National Park, Big Cypress National Preserve, Loxahatchee National Wildlife Refuge, Lake Okeechobee, and other vital wetlands. Once established, these trees form monocultures of dense, impenetrable stands. These stands displace native plant species and are of little use to wildlife. The habitats of at least two endangered animal species, the Florida panther and the Big Cypress fox squirrel, have been diminished by *M. quinqueloria* invasions.

*M. quinqueloria* flowers profusely several times each year. Each seed capsule contains 200 or more seeds and may persist for years. Each tree may harbor millions of seeds. Factors such as fire, herbicidal treatment, cutting, etc., cause desiccation of the capsules and thereby activate massive seed releases. Stand size then increases due to seedling recruitment. Existing control measures are largely ineffective and often exacerbate the problem.

Faunal Inventories

In 1977, Habek (1981) conducted surveys in Australia and New Caledonia and found a large number of insects attacking *M. quinqueloria*. However, many of these were immature and not identifiable. Insects attacking the seeds included a small fly (*Fergusonina sp.; Diptera: Fergusononidae*), a bug (*Euryneus lescheoides* Ashlock; Hemiptera: Lygaeidae*), an unidentified thrips (*Thysanoptera*), and a beetle (*Anobiidae*). The larvae of a moth (*Bathotoma constictana* Meyrick; Lepidoptera: Tortricidae) fed on seed capsules of the related *M. ericifolia* Smith. Unidentified species of Noctuidae, Geometridae, Pyralidae, Tortricidae, and Oecophoridae webbed and fed on flowers and flower buds. Larvae of a gall midge (*Cecidomyiidae*) occurred in the flowers, and a gall-forming eriophyid mite prevented flower formation. Many leaf-feeding insects were found, including at least seven species of Lepidoptera, four species of beetles, gall-making thrips, psyllids, aphids, and scale insects. A gregarious sawfly (*Perga sp.; Hymenoptera: Pergidae*) that was probably host-specific defoliated the trees. Habek (1981) also saw extensive damage caused by a bug (*Ragewellus suspicous* Distant; Hemiptera: Miridae*). Stem-feeding insects included sap-feeding Cercopidae, Membracidae, Eurydema, Psyllidae, Aphididae, Cicadidae, Rriciniidae, and scale insects. Adults of a weevil (*Aterius griseatus* Coleoptera: Curculionidae) were found feeding on saplings. The larvae of this species feed on the roots. An unidentified lepidopteran larva bored stems and killed developing tips.
The Queensland Department of Primary Industries lists the following insects from *Melaleuca* spp.: *A. griseatus, Cryptophaga nephrosea* (Coleoptera: Xylorictidae), *Rhyparida limbatipennis* (Coleoptera: Chrysomelidae), and various scale insects (P. McFadyen, pers. comm.). Species listed in *The Insects of Australia* (CSIRO 1979) include *Sphaerococcus* sp. (Homoptera: Eriococcidae), and *Pteryphoroptera* (Homoptera: Pergidae).

Funds contributed by the USAE, Jacksonville District, and the NPS provided for more complete surveys on *M. quinquenervia*. This exploration was begun in late 1986 from bases in Townsville and Brisbane. To date, over 100 species of insects have been found. Thus far, surveys have been limited to fruit, flower, and foliage-feeding species. Stem-borers and root-feeders haven’t yet been sought, but some twig borers have been found.

Promising species include the sawflies *Perga vollenhovii* Westwood and *Lophyrotoma zonalis* (Rowher). The former gregarious species is heavily parasitized by a tachinid fly. These parasites kill 30 to 80% of the larvae. The latter sawfly regularly defoliates the trees and is perhaps the better candidate. It seems adapted to members of the *M. leucodendra* complex, that, like *M. quinquenervia*, have thick, spongy bark. Larvae burrow into this bark to pupate, rather than in the soil. This would seem an adaptation to wetland habitats and could limit the possible host range of the species.

Many other foliage-feeders have been found. One of the most interesting is a chrysomelid. Both larvae and adults feed on various *Melaleuca* species, mainly on young foliage. The resultant damage is particularly detrimental to seedlings and saplings. In fact, in Darwin this beetle is a pest of container-grown *Melaleuca* plants. An agent that controlled seedlings would be particularly useful in the U.S.A., because seedling recruitment limits the effectiveness of chemical control.

Planthoppers are abundant on *Melaleuca* spp. Insecticidal exclusion of planthoppers from container-grown seedlings appears to accelerate plant growth, so they may be considered further. Numerous species of scale insects associated with the plant also might be useful.

Several insect species feed on flowers and flower buds. Some also damage growing stem tips and others feed on leaf buds. However, few species have been found to feed on seeds or seed capsules. A minute weevil found in dehisced capsules may eat seeds, but this hasn’t been verified.

Several types of galls on *Melaleuca* have been studied but, thus far, only parasitic Hymenoptera have emerged from them. It is unclear whether the gall-formers are heavily parasitized or whether the trophic role of these Hymenoptera is misunderstood.

**Waterlettuce**

Waterlettuce is a free-floating aquatic angiosperm in the arum family (Araceae). Like waterhyacinth, it consists of an emergent rosette of leaves, a short vertical stem (caudex), and submerged roots that hang suspended in the water. The species occurs worldwide in tropical and subtropical regions with no obvious area of origin. It has been present in the U.S.A. since the 18th Century, and some consider it to be native. It was discovered in Florida between 1765-74 (Stuckley and Les 1984). Arguments that it is not native focus upon a supposed lack of seed production in the U.S.A. However, we recently discovered that it produces copious quantities of viable seeds at many south Florida sites (Dray and Center 1989).

Arguments for an exotic origin of this species are better supported by the paucity of specialized herbivores present in the U.S.A. If, as suggested by Waspheere (1981), the center of diversification of a taxon contains the highest number of species highly adapted to that taxon, then the U.S.A. is certainly not within the center of diversification of *Pistia*. We recently conducted statewide surveys of waterlettuce entomofauna (Dray et al. 1988). Herbivores encountered comprised only six species: three moth larvae, a mealy bug, a leathopper, and an aphid. Only one, a root-feeding moth, might be host-specific. By way of contrast, several host-specific insects are associated with waterlettuce in South America.
Weevils, a group well represented in South and Central America (Bennett 1975, Cordo et al. 1978, 1981, DeLoach et al. 1976, Poin de Neiff 1983), were not found in Florida. Several insect species, at least one of which is host-specific, attack waterlutece in Asia (Susa-Ard 1976, George 1963, Joy 1978, Chaudhuri and Janaki Ram 1975, Alam et al. 1980). Although the origin of the waterlutece cannot be ascertained on the basis of available information, it probably isn't native to the U.S.A. The plant was probably introduced early in the history of the U.S.A., possibly from contaminated ballast dumped by ships in rivers or other suitable areas.

Several insect species were studied in South America by USDA and CSIRO researchers for potential use as biological control agents (Cordo et al. 1978, 1981, DeLoach et al. 1976, 1979, Sands and Kasulke 1984, Harley et al. 1984). One of these, the weevil Neohydronomus pulchellus Hustache (Coleoptera: Curculionidae), later proved effective in Australia (Harley et al. 1984) and South Africa (Cilliers 1987). Also, researchers in Thailand and India successfully used a native moth (Namangana pectinicornis Hampson; Lepidoptera: Noctuidae) to control waterlutece (Susa-Ard 1976, George 1963).

Waterlutece is considered a minor weed in the U.S.A. As such, a full scale biological control effort was unjustified. However, waterlutece became more abundant in the Southeast as waterhyacinth decreased. Also, research completed elsewhere facilitated implementation of a less expensive project which we initiated in 1985. Drs. D. Habeck and C. Thompson acquired N. pulchellus from Australia from the CSIRO Long Pocket Laboratories. They also received N. pectinicornis from Thailand by courtesy of Dr. B. Nampopeth. Additional host testing of N. pulchellus confirmed host-specificity, and it was released on 29 April 1987 at Lake Okeechobee. It now is established at five sites in south Florida. Testing of N. pectinicornis is ongoing, but preliminary results have been consistent with data from Thailand and indicate that it is specific (Habeck, pers. comm.). We plan to release it in 1988 or 1989.

Discussion

Biological control of aquatic weeds, particularly floating species, has been uniquely successful. Successful projects include not only alligatorweed, waterhyacinth, and waterlutece but also Salvinia molesta Mitchell (Salviniaeae) (Room et al. 1981). With the exception of alligatorweed, the use of semi-aquatic weevils represents a common link among these projects. Since aquatic weevils are prevalent on hydrilla in Australia and Asia but are absent in the U.S.A., we are hopeful they will prove valuable for control of hydrilla.

Foreign exploration is central to biological control. During the 26-yr history of the aquatic weed program between 1961-87, only six species of biological control agents were released in the U.S.A. In the 10-yr period 1977-87, none were released. Although other factors were involved, this 10-yr hiatus was largely due to the lack of a foreign program. The foreign program was restarted in 1981 and, as a direct result, we released three new species during 1987.

Although foreign research is expensive, unexpected benefits amortize these costs. For example, much of the foreign work on waterlutece was performed by J. DeLoach while he was in Argentina on the waterhyacinth project. These insects were not then being considered for introduction into the U.S.A., but the Australians were interested in them. They continued this work and later developed a successful project. Their studies facilitated development of projects in the U.S.A. and South Africa. We are also able to take advantage of work done by Dr. B. Nampopeth in Thailand on waterlutece. Many countries have likewise capitalized on U.S.A. research on biological control of alligatorweed and waterhyacinth. Australian scientists have assisted several countries with biological control of S. molesta. The relative cost of foreign research quickly diminishes to a pittance for successful projects when the benefits accrue over time and on a global scale.

Our approach towards foreign surveys for biological control agents on hydrilla was based on a desire to acquire as much information as possible with the limited funding available. Our objectives were two-fold. First, we wished to determine by direct observation of native
faunas the best geographical areas in which to conduct research on hydrilla. Second, we wished to inventory the most common species of potential biological control agents from within an extensive unexplored portion of hydrilla’s range. We approached this by conducting short-term surveys at many localities. The surveys successfully documented an abundance of potential biological control agents, which was necessary to justify continuation of the project. However, the surveys were disappointing in that the objectives were not fully achieved. Although the theory behind this approach was sound, logistics proved limiting.

If, as Wapshere (1981) points out, it becomes necessary to explore as much of the range of a pest as possible, the breadth of exploration should be narrowed. With hydrilla, for example, only one of the three herbivore groups commonly encountered (the nymphidine moths) was ubiquitous throughout the Indopacific region. Bagline weevils and Hydrelia flies occurred primarily on mainland areas. Island effects are compounded for aquatics since each water body constitutes an biological island within an island and many islands lack freshwater. Although high levels of endemism are associated with island fauna, a project shouldn’t rely on a search for these endemics. The hydrilla surveys probably would have been equally successful if they had been limited to mainland areas.

A second consideration in the conduct of wide-ranging surveys involves the number of political boundaries encountered. Each country provides unique political and bureaucratic obstacles that usurp precious time. This problem is magnified when several countries are visited during a single trip. If all other factors were equal, it would be wise to choose one or a few countries where the target weed occupies a diversity of habitat types. This would allow more time to be focused upon surveys and less time on bureaucratic matters.

A third consideration should be the amount of time that can be spent in a single country. A minimum duration is required to find sites, collect from them, and the process the collections. Ample time should be allotted to ensure that the target plant is indeed a host of each potential biological control agent encountered. Time should also be allocated to rear immatures to adult stages so that specimens can be identified. If possible, local taxonomists should be consulted immediately to identify as many of the species as possible. Survey trips that are too short may yield only unnamed or unidentified specimens of unconfirmed potential biological control agents. The best that can be hoped for, in this case, is a crude estimate of the number of potential biological control agents extant in an area. The minimum time necessary to accomplish the full objectives should be spent in each area, even if fewer areas can be visited. This requires a flexible approach. If too much time is allocated to an unproductive area, the foreign explorer must be prepared to go elsewhere. The amount and degree of advanced planning required to work in foreign countries is not conducive to flexibility, so experience pays.

Evaluation of biological control agents after field release is important. The degree of success or failure of a biological control agent cannot be ascertained without thorough evaluation. Such studies also test predictions about the potential value of a given biological control agent, and thereby provide feedback for foreign evaluation programs. Experience with waterhacinth has taught us that it is not necessary to prove the effectiveness of a biological control agent to the satisfaction of the most critical skeptics. If a biological control agent is successful, even in a subtle manner, a body of evidence will eventually accumulate that will substantiate this success. The goal rather should be to achieve an understanding of the mechanisms through which the plants and biological control agents interact. Only then can the importance of the biological control agent to the population dynamics of the plant be evaluated correctly.

Determining effectiveness of a biological control agent is not an easy task. When physical damage is highly visible, the role of the biological control agent in the population dynamics of the plant may be overemphasized. If the effects are subtle, they are easily overlooked. Our early success with alligatorweed led to unreasonable expectations for waterhacinth. The alligatorweed flea beetle produced plant damage reminiscent of herbicide treatment. Herbicide applicators who observed this damage were able to appreciate this type of effect. One individual involved in the early field work on alligatorweed (W.C. Durden, pers. comm.), however, feels that the demise of the mats was often due to another species altogether, namely the stem boring moth Vogia mallow Pastrana (Lepidoptera: Pyralidae).
Defoliation by the beetles produced denuded, erect stems but the mat often recovered. Feeding activity of the moth larvae caused the stems to collapse. Their combination was very effective but the flea beetle was credited for the total control obtained. Because the damage caused by the moth was not obvious, its positive attributes never were recognized fully.

In the case of waterhyacinth, although three insects were introduced, credit for control is usually accorded to *N. eichhorniae* because it was the only widespread agent present in Louisiana during the 1970s. However, by the time a substantial plant decline occurred, all three were present. The moth *S. albignutalis* and, to a lesser extent the weevil *N. bruchi* are less persistent than *N. eichhorniae*. When the plants decline from herbivore-induced stress, usually only *N. eichhorniae* is present. Even if the other two species were present earlier and contributed to this decline, their importance to the later fate of the plants is overlooked. All three species play important roles, although their respective effects cannot be easily partitioned from the overall impact. We strongly feel that a complex of natural enemies is advantageous. Nonetheless, if the performance of the three waterhyacinth species were rated, their respective ranks would be the reverse of that expected by DeLoach (1975). Certainly, *N. eichhorniae* should be ranked first. The outstanding attribute of this weevil is its ability to persist. Likewise, the lack of persistence by *S. albignutalis* is its greatest liability.

Waterhyacinth remains overly abundant in the southeastern U.S.A. despite substantial reductions from biological control. Other means of control often must be implemented, especially in critical areas required to be constantly free of weed infestations. However, frequent herbicidal control destabilizes biological control agent populations, rendering them completely ineffective in many critical areas. More research aimed at integrated control and management of biological control agent populations could help achieve better results. Alternatively, additional species of biological control agents might be considered for future introductions.

The various projects that we have discussed broadly have experienced us in the entire spectrum of activities that comprise classical biological control programs. This experience ranges from the preliminary steps of site selection for foreign surveys to the evaluation of efficacy of biological control agents over a 15-yr period. While biological control, like most areas of science, has many widely-accepted principles, we frequently find these to offer little assistance in finding solutions to the practical problems that we face. We must constantly be aware that each plant-herbivore system is unique and be prepared to tailor our programs to their singular and specific attributes.

References


