

1 ALLIGATORWEED

G. R. Buckingham

U. S. Department of Agriculture, Agricultural Research Service, Invasive Plants Research Laboratory, Gainesville, Florida, USA

PEST STATUS OF WEED

Alligatorweed (*Alternanthera philoxeroides* [Mart.] Griseb.) is a South American immigrant that has invaded waterways in the United States, primarily in the southeastern states. It also is a weed in tropical and mild temperate regions around the world. Alligatorweed roots readily along waterways and then grows over the water surface as an anchored floating plant. It also grows terrestrially during dry periods. Alligatorweed is a federal noxious weed and a prohibited or noxious plant in Arizona, California, Florida, and South Carolina (USDA, NRCS, 1999).

Nature of Damage

Economic damage. Alligatorweed disrupts many economic uses of water (Anonymous, 1987; Holm *et al.*, 1997). Thick mats prevent drainage canals, ditches, streams, and other small waterways from emptying rapidly during periods of heavy water load, thus causing flooding (Fig. 1). If mats break loose, they create obstructions by piling up against bridges, dams, and sharp bends in waterways. Thick mats also increase mosquito habitat. Navigation of small waterways is obstructed, as is shoreline navigation in large waterways. Efficiency of irrigation systems is decreased. Fishing and swimming can be affected, although a small fringe of alligatorweed probably benefits fishing. A perusal of various commercial Internet sites in April, 2001 indicated that costs would be approximately \$170 to \$370/ha for control of alligatorweed with the herbicides glyphosate and fluoridone.

Ecological damage. Alligatorweed, like many other invasive aquatic plants, displaces native plants in ditches, along banks, and in shallow water (Holm *et al.*, 1997). Vogt *et al.*, (1992) discussed competition with native plants before and after insect



Figure 1. Alligatorweed mats grow from shore and often cover entire waterways, thereby disrupting water flow and causing flooding. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

biological control agents were released. Alligatorweed disrupts water flow causing increased sedimentation, and it shades submersed plants and animals causing reduced oxygen levels beneath the mat (Quimby and Kay, 1976).

Extent of losses. Current data on the extent of infestation and control costs are lacking. At the beginning of the biological control program in 1963, there were an estimated 65,723 ha of water infested in eight southern states and 26,933 ha of plants in 1970 (Coulson, 1977). The largest infestation, 22,700 ha, was in Louisiana and the smallest, 21 ha, in Mississippi. In 1981, the infestation in the southern states was estimated to have increased, but only because of increases in Texas and Louisiana (Cofrancesco, 1988). All other states reported a decrease. Even though the infestation estimate had tripled in Louisiana, state officials considered biological control to be satisfactory. Much of the increase was due to terrestrial invasion by alligatorweed.

Geographical Distribution

Alligatorweed, a South American native, grows in the coastal plain from Virginia, ca. 37° N, to southern Florida, ca. 25° N, and westward along coastal areas to Texas. It is also found in southern California (Reed, 1970). A distribution map provided by Reed (1970) indicates that the northern limit inland is at about the middle of Alabama, Georgia, and South Carolina, ca. 33.5° N, with an extension slightly further north in the warmer Mississippi Valley, ca. 35° N. However, both southwestern Kentucky, ca. 36.5° N, and Tennessee are included within its range on the USDA PLANTS Database on the Internet (USDA, NRCS, 1999).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Alligatorweed is in the tribe Gomphreneae, subfamily Gomphrenoideae, family Amaranthaceae (Mabberley, 1997), order Caryophyllales, subclass Caryophyllidae (Cronquist, 1988). There are an estimated 170 species of *Alternanthera* in the Western Hemisphere with 120 species in South America alone (Vogt *et al.*, 1979). Less than 5% of the species in South America are amphibious with most being mesophytic or xerophytic. Kartesz (1994) listed 15 species of *Alternanthera*, including ornamentals and immigrants, in the United States and Canada. There are a few species in Asia, mostly introduced from South America. Engler (1934) included *A. philoxeroides* in the subgenus *Telanthera*, section 1. *Alternanthera* can be differentiated from related aquatic species by the opposite, non-succulent leaves; white flowers in short, headlike spikes; and by the presence of a style (Figs. 2, 3). Wain *et al.* (1984) reported two diverse forms of alligatorweed – one with slender stems and short, rounded leaves, and the other with broad stems and long, slender leaves. Their isozyme study indicated that the genetic difference between the forms was similar to the distances reported between subspecies in other plant studies. The importance of these forms in plant invasion and in control efforts has not been investigated. Julien and Broadbent (1980) listed the synonymy for *A. philoxeroides*.



Figure 2. Alligatorweed has opposite, non-succulent leaves. (Photograph courtesy USDA, ARS.)



Figure 3. The white alligatorweed flowers are arranged in stalked, short, headlike spikes, and have a style. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

Biology

Alligatorweed initially roots in wet soil on banks or in shallow water along shorelines and then grows out into waterways. Penfound (1940) reported that beginning in March in Alabama, shoots grew to 38 cm in 1.5 months, to 145 cm in 2.5 months, and to 508 cm in 5.5 months. By September, the mat extended up to 4.6 m away from shore. Alligatorweed is a perennial with hollow stems that buoy the shoots. Floating mats expand over surfaces of all types of waterways and are practically impenetrable. If a waterway dries, alligatorweed changes to a terrestrial form with smaller, tougher leaves and stems. Only vegetative growth has been reported in the United States, although viable seeds have been found in the United

States (Holm *et al.*, 1997). Roots develop at closely spaced nodes along stems. When the stems break, floating sections are able to establish readily on moist soil. Alligatorweed has been reported to reproduce by seeds in South America (Holm *et al.*, 1997).

Analysis of Related Native Plants in the Eastern United States

There are no native *Alternanthera* in the aquatic habitats of the United States. A second introduced species, *Alternanthera sessilis* (L.) R. Br. ex DC., which is pantropical, is reported to be naturalized in the Florida panhandle (Godfrey and Wooten, 1981). As the name implies, the flowers of *A. sessilis* are sessile compared with flowers of alligatorweed, which are stalked. According to Vogt *et al.* (1979), the South American *Alternanthera pungens* Kunth also is established in the United States. Three additional genera in the Amaranthaceae are associated with aquatic habitats. *Amaranthus* has six species in the range of alligatorweed in the southeastern United States, *Iresine* has one species, and *Blutaparion* has one species, *Blutaparion* (= *Philoxerus*) *vermiculare* (L.) Mears or silverhead, which occurs in maritime habitats. Corell and Corell (1972) placed some of the wetland species of *Amaranthus* in the genus *Acnida*. One *Amaranthus* in the eastern United States, *Amaranthus pumilus* Raf. (dwarf or seabeach amaranth) is federally listed as threatened. Its range might overlap with the distribution of alligatorweed biological control agents along the coast of South Carolina, but it is found mostly north of their ranges (Godfrey and Wooten, 1981).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

In 1959, the U.S. Army Corps of Engineers requested that the U.S. Department of Agriculture, Agricultural Research Service evaluate the potential for biological control of alligatorweed (Zeiger, 1967; Buckingham, 1994). Consequently, field surveys and studies of biologies and host ranges of potential biological control agents were conducted in South America (Buckingham, 1996; Coulson *et al.*, 2000). Ultimately, three insect species, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae), *Amynothrips*

andersoni O'Neill (Thysanoptera: Phlaeothripidae), and *Arcola* (as *Vogtia*) *malloi* (Pastrana) (Lepidoptera: Pyralidae, Phycitinae), were introduced into the United States (Coulson, 1977).

Area of Origin of Weed

Alligatorweed is native along the coast of South America from Venezuela to Buenos Aires Province in Argentina (Vogt *et al.*, 1979). It also was reported from the upper and middle Amazon River basin and the Paraná River basin (Vogt *et al.*, 1979). Sites with alligatorweed were most common in Paraguay, Uruguay, and northern Argentina, but this might reflect more intensive surveys for biological control agents in those areas.

Areas Surveyed for Natural Enemies

Annual surveys from 1960 to 1962 covered eastern and northern South America from Argentina to Venezuela, including Trinidad (Coulson, 1977). Additional surveys were conducted in Argentina and Uruguay (Coulson *et al.*, 2000). Surveys also were conducted in the southeastern United States (Coulson, 1977).

Natural Enemies Found

As many as 40 insect species (not all could be identified to species level) were recorded on alligatorweed (Vogt, 1973). Five of the 40 species were considered to suppress alligatorweed (Vogt, 1973). These five were: *A. hygrophila*, *A. andersoni*, *A. malloi*, *Herpetogramma bipunctalis* (F.) (Lepidoptera: Pyralidae), and *Prodenia* sp. (Lepidoptera: Noctuidae) (Maddox *et al.*, 1971; Vogt, 1973). The flea beetle *Disonycha argentinensis* Jacoby (Coleoptera: Chrysomelidae) was later considered a potential agent for control of terrestrial alligatorweed (Cordo *et al.*, 1984). No species able to suppress the weed were discovered in the United States, but native species of *Disonycha* and the moth *H. bipunctalis* were commonly found on alligatorweed in the United States (Vogt *et al.*, 1992).

A fungus native to the United States, *Nimbya* (= *Alternaria*) *alternantherae* (Holcomb and Antonopoulos) Simmons and Alcorn (Hyphomycetes), causes purplish leaf spots and can defoliate plants. However, damage is rarely severe (Holcomb, 1978). In Brazil where it also is native, *N. alternantherae* was not particularly damaging, but

preliminary studies indicated possible potential as a mycoherbicide (Barreto *et al.*, 2000). Damage by a second Brazilian fungus, *Cercospora alternantherae* Ellis and Langlois, was occasionally severe and this species might have potential as a biocontrol agent. (Barreto *et al.*, 2000). A virus-like disease that stunts alligatorweed in Florida has not been studied (Hill and Zettler, 1973).

Host Range Tests and Results

Four insect species were tested in host range experiments in Argentina and Uruguay and in quarantine in Albany, California. Maddox *et al.* (1971) reported that 14 plant species were tested with the alligatorweed flea beetle, but they did not list the species. Buckingham (1996) reported that the 14 species were apparently in 12 genera of eight families. These families were Amaranthaceae, Brassicaceae, Chenopodiaceae, Cucurbitaceae, Malvaceae, Nymphaeaceae, Poaceae, and Polygonaceae. For the flea beetle, *A. hygrophila*, slight adult feeding was found on apical leaves of *Chenopodium ambrosioides* L. and larval feeding and development on *Atriplex patula* var. *hastata* (L.) Gray, but only one malformed adult emerged (Maddox and Resnik, 1969; Maddox *et al.*, 1971). Field observations in South America also played a role in obtaining approval of the flea beetle for introduction into the United States (Anderson, 1963). At least 14 species of aquatic or related plant species in proximity to damaged alligatorweed in Argentina were examined for flea beetles, as were crop plants in the vicinity. No beetles or damage were found.

The alligatorweed thrips, *A. andersoni*, was tested on 21 species in 13 genera of six families (Maddox, 1973). Families were the same as those tested with the flea beetle except Cucurbitaceae and Malvaceae were not tested with the thrips. No development took place in the no-choice and choice experiments except on alligatorweed. Vogt found thrips on the native *Alternanthera hassleriana* Chod. in Argentina (Maddox *et al.*, 1971), but that species has not been reported as naturalized in the United States. Field examinations in Argentina of 46 other plant species in 26 genera of 11 families yielded no *A. andersoni* or its damage (Maddox, 1973).

The alligatorweed stem borer, *A. malloi*, was tested in choice and no-choice tests on 30 plant species in 17 genera of the six families tested with the

thrips (Maddox and Hennessey, 1970). Although there was some feeding on test plants in no-choice tests, development of third or younger instars was restricted to alligatorweed. A few older larvae finished their development on five species in the same amaranth tribe as alligatorweed, Gomphrenae. Field examinations of 51 plant species in Argentina from 1962 through 1967 discovered this moth only on alligatorweed (Maddox and Hennessey, 1970). In South American surveys, moths were reared from *A. hassleriana* and from the closely related *Philoxerus portulacoides* St. Hil. (Vogt *et al.*, 1992). After the moth was released in the United States, it was reared from the native species *Blutaparon vermiculare*, collected in Louisiana and Texas and from subsequent cage tests (Vogt *et al.*, 1992). However, the numbers reared from *Philoxerus* and *Blutaparon*, which are closely related, were small. Pemberton (2000) reported rearing this species from *Alternanthera flavescens* Kunth., a native of coastal hammocks in Florida.

The flea beetle, *D. argentinensis*, was tested on 54 species in 38 genera of 19 families in no-choice larval tests (Cordo *et al.*, 1984). All of the eight families used in tests with *A. hygrophila* were included along with additional families containing crop and ornamental species. Flea beetle larvae fed moderately on four species of Amaranthaceae and two species of Chenopodiaceae, but development to adults was restricted to *Alternanthera paronychioides* St. Hilaire (6.4%) and *Beta vulgaris* L. (3.0%), while 44% completed development on alligatorweed. The development on beets, *B. vulgaris*, prevented release of this species in the United States. Interestingly, Australia tested this species with 36 species in 31 genera of 18 families (Sands *et al.*, 1982). In those tests, no development was observed on beets, but the smaller number of larvae used in the tests (52 versus 234 in the American tests) could have accounted for the slight difference between the two studies. Based upon the American test results (3% development), only one adult would have been expected in the Australian tests and, indeed, one of the 52 larvae did develop to the last instar. Both Australia and New Zealand released this species, but it did not establish (Julien and Griffiths, 1998).

No host range tests were conducted with the other two major biotic suppressants listed by Vogt (1973), *H. bipunctalis* and *Prodenia* sp. The former, the southern beet webworm, also is native to North

America. The latter pupates in the soil, which prevented its use for control of aquatic alligatorweed that was the target of the biological control program (Maddox *et al.*, 1971). If there is future interest in controlling terrestrial alligatorweed, which is commonly eaten by cattle, the *Prodenia* sp. could be studied further although it also attacked *Amaranthus* sp.

Releases Made

Field-collected alligatorweed flea beetles from Argentina were processed through quarantine and released in 1964 in California and South Carolina and in 1965 in Florida (Coulson, 1977). Beetles from Uruguay also were released in South Carolina and a mixed quarantine colony started with beetles from both Argentina and Uruguay was released in Mississippi (1965). Later, beetles collected at release sites, mostly in Florida, were redistributed in Alabama (1967), Arkansas (1969), Georgia (1966), Louisiana (1970), North Carolina (1967), Tennessee (1968), and Texas (1967). Beetles from a quarantine colony held in Gainesville, Florida (of insects originating from Necochea, Argentina) were released in 1979 in Alabama, Florida, North Carolina, and South Carolina (Buckingham *et al.*, 1983).

A quarantine colony of alligatorweed thrips from Argentina was released in Alabama (1968), California (1967), Florida (1967), Georgia (1967), Mississippi (1968), South Carolina (1967), and Texas (1968) (Coulson, 1977).

Eggs from alligatorweed stem borer females collected as larvae in Argentina and held in quarantine were first released in Florida and Georgia in 1971 (Coulson, 1977). Eggs from females collected at Necochea, Argentina, and held in quarantine were released in Georgia and South Carolina in 1972 in an attempt to establish more cold-tolerant populations. Most of the other releases in 1971 and 1972 were from quarantine (Albany) or greenhouse (Gainesville) colonies started with part of the eggs collected in Necochea. Releases were made in the preceding states and in Alabama (1972) and North Carolina (1971).

A handbook that provides instructions for release of the alligatorweed agents was prepared by the U.S. Army Engineer Waterways Experiment Station, based upon the successes of these releases (Anonymous, 1981).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae)

Adults are small (4 to 6 mm long), black and yellow striped beetles that jump when disturbed (Selman and Vogt, 1971). Feeding causes “shot holes” in the leaves, but with heavy adult and larval feeding the leaves are completely eaten, as are upper portions of the stems (Fig. 4). Females deposited clusters of 12 to 54 eggs in two contiguous rows on the underside of apical leaves (Maddox, 1968). The yellowish eggs hatched in four days at 20 to 30 °C. Dark colored larvae ate leaf tissue but often left one epidermis intact, creating a window in the leaf. The three instars developed in eight days at 20 to 30 °C. Mature larvae pupated one to two days after entering stems. The pupal period lasted five days and a pre mating and preoviposition period lasted about six days. The total life cycle from egg to egg was completed in 25 days at 20 to 30 °C. Females lived about 48 days and usually deposited only one egg cluster per day for an average of 1,127 total eggs (Maddox, 1968). Beetles were multivoltine near Buenos Aires, Argentina, producing five generations per year (Maddox, 1968) and probably four to six generations in Florida and the lower Mississippi River Valley (Coulson, 1977; Vogt *et al.*, 1992).



Figure 4. Adults and larvae of the alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt, devour leaves and upper portions of stems. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

Most feeding and oviposition by *A. hygrophila* is on aquatic alligatorweed. Flea beetles, especially larvae, rarely attack plants rooted on shore or in moist ditches. What appears to be typical feeding damage is occasionally observed on terrestrial plants, but it is usually nocturnal feeding by native *Disonycha* flea beetles. In laboratory experiments in Argentina, females oviposited equally on aquatic and terrestrial alligatorweed (Maddox, 1968), but in my experience, females stopped ovipositing almost immediately when fed terrestrial plants. Beetles are specific to alligatorweed and have not been reported on other host plants in the United States even after almost 40 years. A flavone feeding stimulant, 7-a-L-rhamnosyl-6-methoxyluteolin (I), has been isolated from alligatorweed (Zielske *et al.*, 1972) and may be the basis for this specificity.

Alligatorweed thrips, *Amynothrips andersoni* O'Neill (Thysanoptera: Phlaeothripidae)

Adults are small (ca. 2 mm long), black elongate insects with fringed wings (O'Neill, 1968). Larvae, in contrast, are bright orange (Fig. 5). Both feed in the tips of stems where they cause leaf deformation and stunting of the plant (Fig. 6). Often, the edges of leaves curl inwards which provides excellent shelter. Females had a four-day preoviposition period after which they deposited a mean of 201 eggs on hairs in the nodes of the apical leaves (Maddox and Mayfield, 1979). The elongated oval eggs were amber colored. Larval development took eight to 13 days at 24 °C and the whole life cycle from egg to egg required 28 days on average. There were two larval stages, followed by a resting pupal stage on the plant. Unmated females produced only males, but fertilized females produced equal numbers of males and females. Maddox and Mayfield (1972) reported a method for rearing and studying the thrips in the laboratory.

In Argentina, larvae were most abundant in the spring and declined through late summer (Maddox and Mayfield, 1979). Adults were the predominant overwintering stage, although small numbers of larvae and eggs also were present. There were four or five generations, with no reproductive diapause. Predation by spiders and hemipterous insects appeared to be an important regulating factor in Argentina, especially for pupae (Maddox *et al.*, 1971). Dispersal is limited by wing length. Short-winged adults were present in Argentina at most times, but long-winged,



Figure 5. Larvae of the alligatorweed thrips, *Amynothrips andersoni* O'Neill, are bright orange. (Photograph courtesy USDA, ARS.)



Figure 6. Leaf distortion and stunting of the plants is characteristic of feeding by adults and larvae of the alligatorweed thrips, *Amynothrips andersoni* O'Neill. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

dispersing adults were present in the spring (Maddox and Mayfield, 1979). Long-winged forms were believed to be absent in the United States (Coulson, 1977) but were later reported (Buckingham, 1989; Vogt *et al.*, 1992). Unlike the flea beetle, the thrips attacks both aquatic and terrestrial plants, although Maddox *et al.* (1971) reported that it preferred terrestrial plants in Argentina.

Alligatorweed stem borer, *Arcola malloi* (Pastrana) (Lepidoptera: Pyralidae, Phycitinae)

This inconspicuous, light tan moth has a 20 mm wingspan and rests with its folded wings curled partly around its body (Fig. 7). Wing tips lie against the plant, but the head is held aloft with the body at an angle to the plant. Pastrana (1961) provides a more

complete description. Females deposited single white eggs on the undersides of apical leaves (Maddox, 1970). After a preoviposition period of less than 24 hours, moths laid an average of 267 eggs over six to eight days. The eggs hatched in three to four days. Newly hatched larvae tunneled into tips of stems and bored downwards. As they matured, they exited the stems and dropped down on silken threads to bore into other stems. Damaged tips quickly wilted and heavily damaged stems turned yellow and died (Fig. 8). Whitish larvae have wavy, tan, longitudinal stripes. There are five instars that developed in about 24 days (Maddox, 1970). Mature larvae bored through nodes and sealed the holes with masticated tissue apparently to protect against water intrusion. Larvae then



Figure 7. Adults of the alligatorweed stem borer, *Arcola malloi* (Pastrana), are inconspicuous light tan moths that rest with wings held closely to the body. (Photograph courtesy USDA, ARS by Willey C. Durden.)



Figure 8. Stems damaged internally by larvae of the alligatorweed stem borer, *Arcola malloi* (Pastrana), wilt, turn yellow, and die. (Photograph courtesy USDA, ARS.)

chewed exit holes to the outside epidermis, which was left intact as escape hatches for the emerging moths. Amber colored pupae darkened as they developed inside silken cocoons. The life cycle from egg to egg required about 39 days at 23 °C. There were three to four generations per year near Buenos Aires (Maddox, 1970). The moth was multivoltine in the lower Mississippi River Valley, but the number of generations was not determined (Vogt *et al.*, 1992). Brown and Spencer (1973) reported parasitism by *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) on eggs and by *Gambrus* spp. (Hymenoptera: Ichneumonidae) on larvae in newly established populations in Florida.

Both aquatic and terrestrial alligatorweed plants are attacked by *A. malloi*. Stems collapse, turn yellow and die, and heavily damaged mats eventually rot and sink (Brown and Spencer, 1973). Leaves remain on damaged stems, distinguishing stem borer damage from that caused by flea beetles. Vogt *et al.* (1992) discussed the migratory behavior of *A. malloi* in the Mississippi River Valley, where it flew in spring and summer from winter refuges near the Louisiana coast north to Arkansas and northern Mississippi, up to 900 to 1000 km.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Alligatorweed flea beetles did not establish in Arkansas, California, North Carolina, or Tennessee. It was hoped that the population from Necochea, Argentina, might be more cold tolerant than the first beetles released, but there have been no reports of an increase in the flea beetle's range after those 1979 releases. Langeland (1986) reported that releases of the Necochea population were unsuccessful at two study sites in North Carolina. Flea beetles survive mostly in coastal areas or where the mean January temperature is 11.1 °C or higher (Coulson, 1977; Vogt *et al.*, 1992).

Coulson (1977) reported the establishment of alligatorweed thrips in Florida, Georgia, and South Carolina. In 1981, thrips were still present in South Carolina (Buckingham, unpublished data) and in 1982 they were reported in Alabama, Florida, Louisiana, Mississippi, and Texas (Cofrancesco, 1988).

The alligatorweed stem borer successfully established at release sites in all states except Alabama and North Carolina (Coulson, 1977). Later, Cofrancesco (1988) reported it in Alabama and North Carolina as well as in Louisiana, Mississippi, and Texas. Vogt *et al.* (1992) discussed this moth's long distance dispersal ability and noted that in summer it is present in Arkansas.

Suppression of Target Weed

Alligatorweed flea beetle damage was spectacular in the early phases of the program. Vast areas were defoliated (Fig. 9). Mats attacked by the stem borer turned yellow and died (Fig. 10). These two agents have suppressed alligatorweed in much of the warmer parts of its range, so that control efforts are needed only sporadically. In the Carolinas, Tennessee, and the northern regions of the Gulf Coast states, the plant is usually not controlled biologically unless flea beetles are released early in the season from field collections made in Florida or other southern sites. In the Mississippi River Valley, moths and/or flea beetles often migrate north early enough to provide local control (Vogt *et al.*, 1992). Fortunately, alligatorweed is not as invasive at the margin of its range as it is further south.

Cofrancesco (1988) surveyed aquatic plant managers in 1981 about the importance of alligatorweed in ten southern states. None reported that it was a major problem, although some reported locally serious problems, and none reported chemical control efforts directed specifically at it. Chemical controls were usually incidental to waterhyacinth control efforts.

Recovery of Native Plant Communities

There was relatively little evaluation of the biological control of alligatorweed program, mostly because of the speed of the control and the desire to quickly begin programs for biological control of waterhyacinth (*Eichhornia crassipes* [Martius] Solms-Laub.) and hydrilla (*Hydrilla verticillata* [L. f.] Royle). However, Vogt *et al.* (1992) did conduct long term studies in the lower Mississippi River Valley. They reported observations of native plant populations increasing after alligatorweed was suppressed and included tables of the species involved; however, they did not collect quantitative data.



Figure 9. Alligatorweed mats often are completely defoliated by the alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt. Willey Durden collected flea beetles by “walking on water” during the initial establishment phase of the program. (Photograph courtesy USDA, ARS.)



Figure 10. Alligatorweed mats killed by the alligatorweed stem borer, *Arcola malloi* (Pastrana), turn yellow but still retain leaves, in contrast to the yellow stems defoliated by the alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt. (Photograph courtesy USDA, ARS.)

Economic Benefits

Long-term economic benefits of alligatorweed control have not been estimated. The fact that most control efforts are now incidental to waterhyacinth control instead of directed at alligatorweed (Cofrancesco, 1988) suggests substantial benefit from reduced chemical control costs. Undoubtedly, there also are indirect cost savings from reduced ditch and canal clearing and from reduced local flooding. Andres (1977) discussed the costs and benefits of the alligatorweed program, including a 76% reduction

in the hectares treated by the U.S. Army Corps of Engineers and a 92% reduction in weed control costs at one lake in Georgia. However, I am unaware of any newer studies on the costs or benefits of alligatorweed control.

RECOMMENDATIONS FOR FUTURE WORK

Alligatorweed has invaded regions in the United States with climates colder than the native regions in South America. Therefore, there might not be natural enemies suitable for use in the northern parts of alligatorweed's range in the United States. However, more complete control in the warmer areas of the range might be possible by using some of the originally discovered agents that were not pursued or new, as yet, undiscovered agents. Recent surveys in the Amazon River drainage for waterhyacinth insects have located several species that had not been found during earlier surveys (DeQuattro, 2000). A similar situation might be true for alligatorweed. Also, pathogens, both in South America and in the United States, should be more carefully evaluated, especially for their potential to complement insect damage.

Vogt *et al.* (1992) suggested that *Alternanthera* species in Asia should be examined as sources of biological control agents for alligatorweed. Herbivorous insects and pathogens on Asian plants in this genus, if specific both to *Alternanthera* and to aquatic habitats, should be safe for use in the United States and might be more damaging than co-adapted agents from the target plant.

The terrestrial South American flea beetle *D. argentinensis*, which has been released in Australia, should be re-evaluated for its safety and potential use in the United States, if there are no conflicts over control of terrestrial alligatorweed, as there have been in the past (Coulson, 1977). The flea beetle might reduce the invasion of ditches, canals, and shallow ponds when water returns after a drought.

Additional attempts could be made to establish the alligatorweed flea beetle and the stem borer in California, where they did not establish. In the eastern United States, these two species have probably established in all areas where the long-term climate allows. Annual importation from overwintering sites in Florida or coastal areas will be necessary in northern areas of the range, as has been done with

alligatorweed flea beetles by the U.S. Army Corps of Engineers (Zattau, 1989). A supply of these insects should be created for use by agencies and individuals other than the Corps of Engineers.

REFERENCES

- Anderson, W. H. 1963. Status of research on biological control of alligatorweed with insects, unpublished report. U.S. Department of Agriculture, Agriculture Research Service, Beltsville, Maryland, USA; available on request from the Biological Documentation Center, National Agricultural Library, 4th Floor, 10301 Baltimore Boulevard, Beltsville, Maryland, 20705-0000).
- Andres, L. A. 1977. The economics of biological control of weeds. *Aquatic Botany* 3: 111-123.
- Anonymous. 1981. *The use of insects to manage alligatorweed*. Instruction Report A-81-1. U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi, USA.
- Anonymous. 1987. Alligatorweed - a monster of a problem. *Landscape Management* 25: 94, 108.
- Barreto, R., R. Charudattan, A. Pomella, and R. Hanada. 2000. Biological control of neotropical aquatic weeds with fungi. *Crop Protection* 19: 697-703.
- Brown, J. L. and N. R. Spencer. 1973. *Vogtia malloi*, a newly introduced phycitine moth (Lepidoptera: Pyralidae) to control alligatorweed. *Environmental Entomology* 2: 519-523.
- Buckingham, G. R. 1989. Macropterous adults of alligatorweed thrips, *Amylothrips andersoni* O'Neill, found in Florida. *Florida Entomologist* 72: 221-223.
- Buckingham, G. R. 1994. Biological control of aquatic weeds, pp. 413-479. In Rosen, D., F. D. Bennett, and J. L. Capinera (eds.). *Pest Management in the Subtropics: Biological Control - the Florida Experience*. Intercept, Andover, Hampshire, United Kingdom.
- Buckingham, G. R. 1996. Biological control of alligatorweed, *Alternanthera philoxeroides*, the world's first aquatic weed success story. *Castanea* 61: 231-243.
- Buckingham, G. R., D. Boucias, and R. F. Theriot. 1983. Reintroduction of the alligatorweed flea beetle (*Agasicles hygrophila* Selman & Vogt) into the United States from Argentina. *Journal of Aquatic Plant Management* 21: 101-102.
- Cofrancesco, A. F., Jr. 1988. *Alligatorweed survey of ten southern states*. Miscellaneous Paper A-88-3. U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi, USA.

- Cordo, H. A., C. J. DeLoach, and M. Ferrer. 1984. Biology and larval host range of the flea beetle *Disonycha argentinensis* (Coleoptera: Chrysomelidae) on alligatorweed in Argentina. *Annals of the Entomological Society of America* 77: 134-141.
- Corell, D. S. and H. B. Corell. 1972. *Aquatic and Wetland Plants of Southwestern United States*. Vol. II. Stanford University Press, Stanford, California, USA.
- Coulson, J. R. 1977. *Biological control of alligatorweed, 1959-1972. A review and evaluation*. Technical Bulletin 1547. U.S. Department of Agriculture, Agricultural Research Service,
- Coulson, J. R., P. V. Vail, M. E. Dix, D. A. Nordlund, and W. C. Kaufmann (eds.). 2000. *110 Years of Biological Control Research and Development in the United States Department of Agriculture: 1883-1993*. U.S. Department of Agriculture, Agricultural Research Service. Washington, D. C.
- Cronquist, A. 1988. *The Evolution and Classification of Flowering Plants*, 2nd ed. New York Botanical Garden, Bronx, New York.
- DeQuattro, J. 2000. Watch out water-hyacinth! new jungle enemies are coming. *Agricultural Research* 48: 10-12.
- Engler, A. 1934. *Die natürlichen Pflanzenfamilien*. Vol. 16C, *Angiospermae, Riehe Centospermae*, 2nd ed. Verlag von Wilhelm Engelmann, Leipzig, Germany.
- Godfrey, R. K. and J. W. Wooten. 1981. *Aquatic and Wetland Plants of Southeastern United States. Dicotyledons*. University of Georgia Press, Athens, Georgia, USA.
- Hill, H. R. and F. W. Zettler. 1973. A virus-like stunting disease of alligatorweed from Florida. *Southern Abstracts* 443.
- Holcomb, G. E. 1978. *Alternaria alternanthereae* from alligatorweed is also pathogenic on ornamental Amaranthaceae species. *Phytopathology* 68: 265-266.
- Holm, L., J. Doll, E. Holm, J. Pancho, and J. Herberger. 1997. *World Weeds: Natural Histories and Distribution*. John Wiley and Sons, New York.
- Julien, M. H. and J. E. Broadbent. 1980. The biology of Australian weeds. 3. *Alternanthera philoxeroides* (Mart.) Griseb. *Journal Australian Institute of Agricultural Science* 46: 150-155.
- Julien, M. H. and M. W. Griffiths (eds.). 1998. *Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds*, 4th ed. CAB International, Wallingford, United Kingdom.
- Kartesz, J. T. 1994. *A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland*. Vol. 1. *Checklist*. Timber Press, Portland, Oregon, USA.
- Langeland, K. A. 1986. *Management program for alligatorweed in North Carolina*. UNC-WRRI-86-224. Water Resources Research Institute, University of North Carolina, Raleigh, North Carolina, USA.
- Mabberley, D. J. 1997. *The Plant Book*, 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- Maddox, D. M. 1968. Bionomics of an alligatorweed flea beetle *Agasicles* sp., in Argentina. *Annals of the Entomological Society of America* 61: 1299-1305.
- Maddox, D. M. 1970. The bionomics of a stem borer, *Vogtia malloi* (Lepidoptera: Phycitidae), on alligatorweed in Argentina. *Annals of the Entomological Society of America* 63: 1267-1273.
- Maddox, D. M. 1973. *Amynothrips andersoni* (Thysanoptera: Phlaeothripidae), a thrips for the biological control of alligatorweed. I. host specificity studies. *Environmental Entomology* 2: 30-37.
- Maddox, D. M. and R. D. Hennessey. 1970. The biology and host range of *Vogtia malloi* Pastrana, unpublished report. U.S. Department of Agriculture, Agricultural Research Service, Entomological Research, Entomological Research Division, Albany, California, USA; available on request from the Biological Documentation Center, National Agricultural Library, 4th Floor, 10301 Baltimore Boulevard, Beltsville, Maryland, 20705-0000)
- Maddox, D. M. and A. Mayfield. 1972. A method for rearing and studying *Amynothrips andersoni* in the laboratory. *Journal of Economic Entomology* 65: 1521-1523.
- Maddox, D. M. and A. Mayfield. 1979. Biology and life history of *Amynothrips andersoni*, a thrip for the biological control of alligatorweed. *Annals of the Entomological Society of America* 72: 136-140.
- Maddox, D. M. and M. E. Resnik. 1969. Determination of host specificity of the alligatorweed flea beetle, *Agasicles* n. sp., with radioisotopes. *Journal of Economic Entomology* 62: 996-999.
- Maddox, D. M., L. A. Andres, R. D. Hennessey, R. D. Blackburn, and N. R. Spencer. 1971. Insects to control alligatorweed: an invader of aquatic ecosystems in the United States. *Bioscience* 21: 985-991.
- O'Neill, K. 1968. *Amynothrips andersoni*, a new genus and species injurious to alligatorweed. *Proceedings of the Entomological Society of Washington* 70: 175-183.
- Pastrana, J. A. 1961. Una nueva Phycitidae (Lep.) parasito de la "lagunilla. *Revista de Investigaciones Agrícolas* 15: 265-272.
- Pemberton, R. W. 2000. Predictable risk to native plants in weed biological control. *Oecologia* 125: 489-494.
- Penfound, W. T. 1940. The biology of *Achyranthes philoxeroides* (Mart.) Standley. *American Midland Naturalist* 24: 248-252.

- Quimby, P. C., Jr. and S. H. Kay. 1976. Alligatorweed and water quality in two oxbow lakes of the Yazoo River basin. *Journal of the Mississippi Academy of Science* 21 (supplement): 13.
- Reed, C. F. 1970. *Selected Weeds of the United States*. Agriculture Handbook 366. U.S. Department of Agriculture, Agricultural Research Service.
- Sands, D. P. A., R. C. Kassulke, and K. L. S. Harley. 1982. Host specificity of *Disonycha argentinensis* [Col: Chrysomelidae], an agent for the biological control of *Alternanthera philoxeroides* (alligator weed) in Australia. *Entomophaga* 27: 163-172.
- Selman, B. J. and G. B. Vogt. 1971. Lectotype designations in the South American genus *Agasicles* (Coleoptera: Chrysomelidae), with description of a new species important as a suppressant of alligatorweed. *Annals of the Entomological Society of America* 64: 1016-1020.
- USDA, NRCS. 1999. United States Department of Agriculture, Natural Resources Conservation Service. Plants Database <http://plants.usda.gov> (accessed January 2001).
- Vogt, G. B. 1973. Exploration for natural enemies of alligator weed and related plants in South America, appendix B, pp. 1-66. In Gangstad, E. O., R. A. Scott, Jr., and R. G. Cason (eds.). *Biological Control of Alligatorweed*. Technical Report 3. U.S. Army Engineer Waterways Experiment Station, Aquatic Plant Control Program. Vicksburg, Mississippi, USA.
- Vogt, G. B., J. U. McGuire, Jr., and A. D. Cushman. 1979. *Probable evolution and morphological variation in South American disonychine flea beetles (Coleoptera: Chrysomelidae) and their amaranthaceous hosts*. Technical Bulletin 1593. U.S. Department of Agriculture, Agricultural Research Service, Washington, D.C.
- Vogt, G. B., P. C. Quimby, Jr., and S. H. Kay. 1992. *Effects of weather on the biological control of alligatorweed in the lower Mississippi Valley region, 1973-83*. Technical Bulletin 1766. U.S. Department of Agriculture, Agricultural Research Service, Washington, D.C.
- Wain, R. P., W. T. Haller, and D. F. Martin. 1984. Genetic relationship among two forms of alligatorweed. *Journal Aquatic Plant Management* 22: 104-105.
- Zattau, W. C. 1989. Aquatic plant control operations support center, pp. 304-306. *Proceedings 23rd Annual Meeting Aquatic Plant Control Research Program*, November 14-17, 1988, West Palm Beach, Florida. Miscellaneous Paper A-89-1. U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi, USA.
- Zielske, A. G., J. N. Simons, and R. M. Silverstein. 1972. A flavone feeding stimulant in alligatorweed. *Phytochemistry* 11: 393-396.
- Zeiger, C. F. 1967. Biological control of alligatorweed with *Agasicles* n. sp. in Florida. *Hyacinth Control J.* 6: 31-34.