

ABSTRACT: The introduction of insects or pathogens has safely controlled many weeds in over 50 countries during the past 100 years. In Hawaii, nine weeds have been completely or substantially controlled since 1902. In continental North America since 1945, St. Johnswort (Hypericum perforatum), puncturevine (Tribulus terrestris), tansy ragwort (Senecio jacobaea), musk thistle (Carduus thoermeri), and skeletonweed (Chondrilla juncea) have been controlled in rangelands; and alligatorweed (Alternanthera philoxeroides) and waterhyacinth (Eichhornia crassipes) have been controlled in aquatic areas. Prospects are good for successful control of knapweeds and yellow starthistle (Centaurea spp.), leafy spurge (Euphorbia esula), toadflaxes (Linaria spp.), and snakeweeds (Gutierrezia spp.) in rangelands; for waterlettuce (Pistia stratiotes) and hydrilla (Hydrilla verticillata) in aquatic sites; and for melaleuca tree (Melaleuca quinquenervia), purple loosestrife (Lythrum salicaria), Brazilian peppertree (Schinus terebinthefolius), and saltcedar (Tamarix spp.) in natural areas. Many other weeds have potential for biological control. Biological control reduces the abundance of selected weeds but does not harm nontarget (including rare) species; it is nonpolluting. Because of its permanence and relative low cost, the introductory approach is more appropriate in natural areas than is augmentation. The ecological consequences of biological control of pests and of vegetation change in natural areas, and future opportunities and directions for biological control of weeds are discussed.

ECOLOGICAL CONSIDERATIONS

A weed is usually defined as any plant that is objectionable or interferes with the activities or welfare of humans (Weed Science Society of America 1985). Since this is not a taxonomic or ecological definition, it can be modified to suit particular situations. For example, a weed in rangelands may be any plant that is not palatable and nutritious to livestock from the rancher's point of view. A weed of natural areas, from the nature conservationist's point of view, might be any non-native plant.

Weed control is a pertinent topic for those concerned with natural areas because invading exotic weeds cause unwanted changes in the plant and animal communities and because the broad-spectrum herbicides used to control weeds are detrimental to many nontarget (including rare) species.

The categorization of weeds as "introduced" or "native" is useful to those involved in biological control and to natural areas managers. This is less important to those interested in crops or in chemical control methods. Both introduced and native weeds can be very damaging in certain ecosystems and both can be controlled by the introduction of additional herbivores, especially of

those that are specific to the weed.

Introduced plants often increase to high densities (become weeds) because of the lack of herbivores that feed on them, especially of the herbivores that coevolved with them. Introduced weeds have been transferred from their native ranges to North America or to other continents primarily as ornamentals, as contaminants in livestock feed, and as contaminants in crop and pasture seeds. New introductions could result from the activities of tourists wishing to try a new plant as an ornamental, dealers of aquarium plants, and even agricultural researchers introducing plants for breeding or for forage crops. Strict quarantine inspection and control and public education are essential to prevent the introduction of the many serious foreign weeds that still have not reached North America.

Some species of both introduced and native plants have increased and others have decreased greatly in density as a result of human-caused changes in the ecosystem such as the clearing of forests and grasslands for agriculture, residences, and highways; the introduction of grazing livestock; the suppression of fires; and, recently, by acid rain. Increasing levels of CO₂ are known to stimulate plant growth. New evidence

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indicates that in an atmosphere of higher CO₂, woody species that have a C3 carbon metabolic pathway have a competitive advantage over warm-season grasses that have a C4 pathway. This suggests that the recent increase in atmospheric CO₂ could be a major contributing factor to the worldwide conversion of grasslands to shrubland (Mayeux et al. in press).

Certain weeds might be reduced in density by reversing the action that caused their increase, but this may be unacceptable to large segments of society. For example, native poison ivy (*Toxicodendron* spp.) and ragweeds (*Ambrosia* spp.) could be reduced by returning cleared areas to the original unbroken forests. Many native range weeds might be reduced by discontinuing grazing.

Many of these plants that have increased greatly in abundance are regarded by some people as weeds needing control and by other people as beneficial plants. Thus a "conflict of interest" is created (Huffaker 1959, Turner 1985). For example, mesquite (Prosopis spp.) is a weed to ranchers but is a desirable tree for homeowners, barbecue wood producers, and beekeepers (DeLoach 1985). To conservationists, saltcedar (Tamarix sp.) is a plague because it displaces native vegetation, birds, and mammals; but it is valuable to white-winged dove hunters and beekeepers (DeLoach 1990a). Johnson grass (Sorghum halepense) is a serious weed in crops but is used for grazing and hay. Poison ivy (Habeck 1990) and ragweeds (DeLoach 1990b) cause serious medical problems for millions of susceptible people, but their seeds are valuable food for songbirds (Martin et al. 1951).

Smeins (1983) and Johnson (1985) pointed out that the species composition of plant communities has always been in flux and that it continues to change today, from both natural and human causes. The concept of maintaining "natural" areas in their pristine condition, uninfluenced by human actions, is probably unrealistic in absolute terms. Johnson (1985) doubted that any patch of vegetation on earth was completely free of human influence; even the presettlement North American landscape was influenced by native American cul-

tures. Also, great changes have occurred in recent times that are independent of any human action. Eastern hemlock (Tsuga canadensis) increased, declined, and increased again between 13,000 and 2000 years ago. Creosotebush (Larrea tridentata) was introduced (possibly by birds) ca. 14,000 years ago. These are two examples of naturally occurring and relatively recent changes to North American vegetation. Johnson (1985) pointed out that current theoretical research on the nature of vegetation suggests that the Gleasonian individualistic hypothesis of a dynamic, everchanging system more closely reflects reality than does the Clementsian theory of climax vegetation in delicately balanced, coevolved ecosystems (where each species has its own place) that are stable through time. Johnson demonstrated that in spite of several recorded changes in composition of dominant species, ecosystem function always recovered rapidly and has remained stable in terms of nature's "services" provided, although the specific "goods" may shift from one species to another.

Nevertheless, the rate of change has increased greatly during the last 100 to 200 years and has become global, with air pollution and the increase in atmospheric CO₂. The leading tenet of the conservationist movement is that species diversity is desirable. Many species of plants and animals are becoming extinct in many areas of the world. This loss of species diversity is one of the most important and alarming processes of environmental change because it is wholly irreversible. The lost biota represents a lost potential source for new foods, medicines, and other commercially important substances (Wilson 1989). It also represents a vast reserve of genetic variability with the potential for adaptation to future ecological changes. Egler (1984) pointed out the value of maintaining natural areas as free as possible of human influence, although change will continue even here. Natural areas provide a standard that, by comparison with all managed areas, allows us to judge and separate the role of humans in the total environment.

Biological control of undesirable weeds can contribute to the conservation of natural areas because it is much less intrusive than the broad-spectrum chemical and mechanical controls presently in use. It is also a positive alternative to doing nothing and allowing a few species of weeds to dominate.

For the purposes of this discussion, I will define biological control of weeds as the planned use of undomesticated organisms (usually insects or plant pathogens) to reduce the vigor, reproductive capacity, or density of weeds. This definition is similar to that used by Harris (1988). It excludes cultural controls (grazing management, crop rotation, etc.) and natural control (the action of organisms without human direction). Biological control is highly specific to the target weed, it has little or no effect on nontarget plants, and it causes no pollution. It is very economical for use in natural areas (Andres 1977, Harris 1979, DeLoach et al. 1986). Although the method involves the introduction of yet another foreign organism, the control agent itself, this is acceptable in natural areas because biocontrol acts to shift vegetative species composition and biomass back to native species, even though the control agent remains. The objective of biological control is not to eradicate the weed but to reduce its density below the economic threshold, or, in natural areas, below some biological threshold so that other controls are not needed — or at least so that damage and the use of other controls are reduced. Biological control of weeds has never resulted in the complete removal of a species from an ecosystem or in making rare plant species more rare (Harris 1988).

Biocontrol of weeds in other ecosystems also affects natural areas because an introduced biocontrol agent has the potential to spread throughout its area of climatic tolerance if its host plant exists there. Natural areas, therefore, cannot be considered separately from agricultural areas, or vice versa, when a biocontrol program against a weed that occurs in both areas is considered.

Biological control always has ecological consequences, but so has any pest control method or the do-nothing option (Harris 1990a). The challenge is to distinguish beneficial changes from harmful ones, and to use our knowledge and technology to

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improve on the present situation.

The effect of dense stands of weeds in a natural community is decreased plant diversity: the weed occupies most of the plant community (Harris 1988) and excludes native plants and animals from their habitats. This frequently happens in the absence of consumer (herbivore) pressure. In several cases, species diversity has increased greatly when an herbivore was added or decreased when an herbivore was removed (Harris 1988). In California, the number of plant species present in affected rangelands increased by 35% following biological control of St. Johnswort (Klamath weed, Hypericum perforatum) (Huffaker and Kennett 1959).

Harris (1988) postulated that because of the density-dependent nature of the herbivore-host plant relationship, attack by introduced biological control agents on a low-density plant is very unlikely. In fact, he suggested that rare and endangered plant species faced far greater risk of extirpation through competition with too abundant weeds, or the herbicides used to control them, than from an introduced biological control agent. Harris (1990a) cited cases in the United States where rare species, such as the northern prairie skink (Eumeces septentrionalis) and the western prairie fringed orchid (Platanthera praeclara), were becoming rarer because of invading weeds. In Australia, over 50 plant species are considered endangered because introduced weeds out-compete them (Bell 1983). In Germany, 89 of 589 rare plants are declining as a result of herbicide applications (Sukopp and Trautmann 1981).

Biological control by the introduction of foreign control organisms, because of its areawide effect, counteracts the areawide causes of weed increase — livestock grazing, repression of fires, eutrophication of bodies of water, possibly the effect of increasing atmospheric CO₂, and the vast increase in disturbed areas and edges caused by human settlement and agriculture. In terms of methodology and ecological theory, biological methods could be used to control both introduced and native weeds; however, past efforts have been directed almost entirely against introduced species.

The two primary factors limiting the application of biological control are (1) whether conflicts of interest between the harmful and beneficial values of the weed can be resolved and (2) whether or not suitable control organisms can be found.

In the following discussion, I emphasize biological control of introduced weeds since native plants seldom are considered weeds in natural areas.

APPROACHES TO BIOLOGICAL CONTROL OF WEEDS

Two major approaches have been utilized in biological control of weeds (Huffaker 1958). Introduction of foreign natural enemies has been most often used in the past. This method gives permanent control. The cost of a program, \$1-2 million in 1979 values, is only that of the research and distribution of the organisms; the individual farmer or rancher incurs no direct costs. Cost remains constant regardless of the area treated, but cost per hectare decreases as larger areas are controlled and decreases still more with each added year of control. This makes the method applicable to areas of low economic return, such as rangelands and natural areas (DeLoach et al. 1986). Benefit-cost ratios for successful projects typically exceed 50:1 (Andres 1977, Harris 1979). Benefit-cost ratios for herbicidal or mechanical controls in rangelands typically are less than 3:1. A disadvantage of introduction is that the control organisms are likely to attack the weed in areas where it has beneficial value.

The second approach is to augment the effectiveness of the phytophagous organisms already present in an area, whether native or previously introduced. These methods include inundating the area with insects (Frick and Chandler 1978) or plant pathogens used as "bio-herbicides" (Templeton and Smith 1977), modifying the agro-ecosystem to the disadvantage of the weed, and using insecticides or hyperparasites to reduce the parasites or predators that attack the biocontrol agent.

The greatest advantage of augmentation is that it is active only where applied and so does not damage the plant in areas where it

is considered beneficial. Also, augmentation's effect can be ended simply by discontinuing applications. The method is similar to herbicidal control in that the entire affected area must be treated at repeated intervals and so cost is dependent on the area treated and the duration that control is needed. Augmentation is unlikely to be economical in areas of low economic return such as rangelands and natural areas (DeLoach et al. 1986). However, plant pathogens can be mass produced much more economically than insects. Augmentation using pathogens may be possible if the exacting climatic conditions required for infection and disease development can be met in the field.

REGULATIONS AND SAFEGUARDS

Biological control of weeds entails potentially serious dangers, particularly of attack by the control agent on nontarget plant species and attack on the target weed in areas or situations where control is not wanted (Huffaker 1958). The basic protocol of foreign exploration, foreign testing, quarantine testing in the country of introduction; release and establishment in the field; and evaluation has been established and refined by many workers over the years (Huffaker 1957, Zwölfer and Harris 1971, Harris 1973, Wapshere 1975, Sands and Harley 1981, and Goeden 1983).

In the United States, the Technical Advisory Group for the Introduction of Biological Control Agents for Weeds (TAGIBCAW) reviews research on the introduction of natural enemies for biological control of weeds and makes recommendations to the Animal and Plant Health Inspection Service (APHIS) of the U.S. Department of Agriculture. APHIS regulates and issues permits for this research (Klingman and Coulson 1982, Coulson and Soper 1989, Lima 1990). TAGIBCAW consists of a multidisciplinary, 13-member committee that includes weed scientists. entomologists, plant pathologists, botanists, and wildlife scientists representing the Agricultural Research Service (ARS)-National Program Staff, APHIS-Plant Protection and Quarantine, U.S. Forest Service and the Cooperative State Research Service (CSRS) of the U.S. Department of

Agriculture; Fish and Wildlife Service, National Park Service, Bureau of Land Management, and Bureau of Reclamation of the U.S. Department of the Interior; U.S. Army Corps of Engineers; National Plant Board; Environmental Protection Agency; and the Weed Science Society of America.

At the beginning of a weed control project, TAGIBCAW provides the researcher an opinion on the conflicts of interest between the beneficial and harmful values of the weed and determines whether or not an introductory biological control program should proceed. After a candidate control organism is found and tested overseas, TAGIBCAW reviews the test results and recommends whether or not the organism may be introduced into quarantine in the United States or what additional testing is required. Introduction into quarantine requires state approval and an APHIS permit. Further testing and the production of clean colonies for release is then done in a quarantine facility and with personnel and procedures approved by APHIS. TAGIBCAW again reviews these results before recommending the release (or not) of the control agent. Release from quarantine into the field requires permission from the departments of agriculture in the states in which releases will be made and another permit from APHIS. Canada has an approval system similar to that of the United States. Agreement is sought, although not required, by the other border country if either the United States, Canada, or Mexico proposes the release of a weed-controlling organism foreign to North America.

HISTORY AND WORLDWIDE USAGE

Biological control of weeds is a tried and proven technology, backed by over 100 years of investigations and applied in more than 50 countries (Julien 1987). The first planned use of an undomesticated organism to control a weed occurred before 1865 in Ceylon when scale insects of the genus *Daclylopius* from South America were introduced and provided excellent control of a species of introduced South American prickly pear cactus (*Opuntia* sp.). Since the early 1900s, there has been a concentrated research effort on biocontrol of introduced

weeds by the introduction of foreign natural enemies. This research began in 1902 in Hawaii to control lantana (*Lantana camara*). A serious effort began in Australia in 1913 to control prickly pear cactus (Dodd 1940). Research in the mainland United States began in 1945 (Goeden 1978, Julien 1987).

DeBach (1974) calculated that of the 41 projects (weeds) attempted worldwide, 75% had achieved a measurable degree of success: 8 were completely successful, 9 achieved substantial control, 14 achieved partial control, and 10 achieved no control. Through 1987, control had been attempted for 94 weed species in 53 countries, a total of 610 projects (insect-weed pairs) (Julien 1987). Foreign insects have been released to control 32 weed species in Australia, 28 in the United States, 19 in Hawaii, 18 in South Africa, 15 in Canada, 11 in New Zealand, 11 in India, 7 in Fiji, 3-6 in 11 countries, 2 in 12 countries, and 1 weed in 22 countries. The percentage of weeds successfully controlled is now lower because many new projects have been initiated that have not had sufficient time to succeed.

A few organizations have done most of the basic research, including overseas exploration and testing. ARS of the U.S. Department of Agriculture has conducted research since 1945 and has had permanent laboratories in Rome since 1958, Buenos Aires since 1962, and in Japan-Korea since 1972. In 1989, ARS opened laboratories in Beijing, China, and Moldavia, USSR. The Canadian Department of Agriculture, centered at Regina, Saskatchewan has long worked on control of rangeland weeds of joint interest with the United States. Others are the Hawaiian Department of Agriculture (HDA); the Commonwealth Institute of Biological Control (CIBC) with permanent laboratories in Trinidad, India, Pakistan, and Switzerland; the Australian Scientific and Industrial Research Organization (CSIRO); the Queensland Department of Lands near Brisbane, Australia; the Plant Protection Research Institute of the Department of Agricultural Development and the University of Capetown, Union of South Africa; and the Department of Scientific and Industrial Research, New Zealand. Various universities and other government agencies have played important roles in

several projects in all of these regions. The Commonwealth countries often obtain much of their overseas research through the CIBC. Natural enemies developed by one country are often exchanged or shared with other countries. This has been of great value to all countries but especially to those that lack funding for the long-term research programs needed to develop new control agents.

Several reviews describe the theory and current progress of projects: in the United States (Huffaker 1959, 1964; Holloway 1964), for aquatic weeds (Brezonik and Fox 1975, Andres and Bennett 1975), in Canada (Kelleher and Hulme 1984), internationally (Andres et al. 1976, Laing and Hamai 1976, Goeden 1978, Schroeder 1983, Julien 1987), in a series of international symposia on biological control of weeds (Freeman 1978; Delfosse 1981, 1985, 1990), and by the use of pathogens (Templeton et al. 1979, Charudattan and Walker 1982).

Biological control of weeds research in North America can be discussed by geographic regions, most of which have a group of weeds of importance primarily in that area.

Hawaiian Rangeland Weeds

In 1902, 14 species of insects (all from Mexico) were released to control lantana in Hawaii. Eight became established and provided control, although not in all areas. Three species were released in 1925 and 1926 on nutsedge (*Cyperus rotundus*) and gorse (*Ulex europaeus*), but these gave no control. Interest revived in the 1950s after the success of St. Johnswort (*Hypericum perforatum*) control in California. Eight additional insects were released on lantana and five of these gave substantial to complete control in many areas (Goeden 1978, Julien 1987).

During the period from 1945 to 1965, research was expanded by HDA and natural enemies were introduced to control 18 weed species. After the late 1960s, little work was done on biocontrol using insects as control agents until 1986 when research on gorse (Markin and Yoshioka 1990) and

other weeds was resumed by HDA and the U.S. Forest Service. Of a total of 20 weed species for which biocontrol was attempted in Hawaii, 9 species have been completely or substantially controlled—a success rate of 45%. A total of 63 species of insects were released and 43 became established (Goeden 1978, Julien 1987). Weeds that were completely or substantially controlled were lantana, crofton weed (Ageratina adenophora), hamakua pa-makani (A. riparia), prickly pear cactus (Opuntia ficus-indica), three-cornered jacks (Emex australis), lesser jacks (E. spinosa), puncturevines (Tribulus terrestris and T. cistoides), and St. Johnswort.

More recently, scientists at the University of Hawaii investigated plant pathogens as biocontrol agents. In 1975, Cercosporella sp. from Jamaica was released on Oahu to control the introduced pasture weed hamakua pa-makani. Control has been spectacular in zones of high rainfall and optimal temperatures for disease development, with greater than 95% control achieved during the first year after release. In areas with less than optimal rainfall and temperature conditions, control has been less than 80%. More than 50,000 ha of pastureland now has been rehabilitated to its full production potential (Trujillo 1985). This was the first, and most successful, control of a weed in the United States using an introduced plant pathogen. Recent research indicates that Koster's curse (Cledemia hirta) might be controlled with the plant pathogen Colletotrichum sp. from Panama (Trujillo et al. 1986).

Weeds of Western Rangelands

Research in the northwestern United States and western Canada has concentrated on weeds that were introduced from and have their site of origin in Eurasia. Biological control has been attempted for 23 species of weeds of rangelands. Seven of these (29%) have been completely or substantially controlled in large areas. Additional insects have recently been approved for control of other weeds, and other promising insects are under study (Goeden 1978, Kelleher and Hulme 1984, Julien 1987). Several foreign plant pathogens have been found that appear specific to several weed

species (Templeton 1982, Défago et al. 1985, Bruckart and Dowler 1986, Bruckart 1990).

The first biocontrol project for a weed in North America was the effort to control St. Johnswort (or Klamath weed) in California. This poisonous weed was introduced from Europe and by the 1940s, ca. 2 million ha of western U.S. and Canadian rangelands were densely infested and the cattle industry was severely threatened. It was also introduced into Australia in the 1880s and biological control research began there in 1926. Two species of European leaf beetles (Chrysolina quadrigemina and C. hyperici) were obtained from Australia and released in California in 1945-46. Two other insects, imported into California directly from France, were released in 1950: Agrilus hyperici, which bores into the roots, and Zeuxidiplosis giardi, which forms leafbud galls (Julien 1987). The results were spectacular. Within ten years, St. Johnswort was reduced to an occasional roadside plant in California (Holloway 1964), although control is still incomplete in Idaho, Montana, and some other northern areas. These insects were released in Canada in the 1950s and in Hawaii in the 1960s (Goeden 1978, Julien 1987). The geometrid Anaitis plagiata was released in 1976 in Montana and in Canada (Julien 1987).

Since the 1960s, 18 species of insects have been introduced from Europe (13 have become established) in either or both the United States and Canada to control a complex of 11 species of thistles and knapweeds in five genera (Harris 1971, 1984a; Frick 1978; Batra et al. 1981; Julien 1987).

For musk thistle (Carduus thoermeri), a seed head weevil (Rhinocyllus conicus) was introduced first (1968) and has reduced stands by 80–99% over large areas of Montana (Rees 1978), Virginia (Kok 1990), Missouri (Puttler 1989), and Canada (Harris 1984b), and control is increasing in several other states. A rosette weevil (Trichosirocalus horridus) released in 1974 is providing additional damage to plants in Virginia and Missouri and is established in Wyoming. R. conicus also attacks plumeless thistle (Carduus acanthoides), Italian thistle

(C.pycnocephalus), bull and Canada thistle (Cirsium vulgare and C. arvense), other Carduus species, and milk thistle (Silybum marianum) but provides less control of these. A root-feeding syrphid fly (Cheilosia corydon) from Europe was released by the Maryland Department of Agriculture in 1990 (N. Rees, pers. comm. 1991). A European rust (Puccinia carduorum) also shows promise for biocontrol of musk thistle (Politis and Bruckart 1986, Bruckart 1990).

Most of the early research on spotted and diffuse knapweeds (Centaurea diffusa and C. maculata) was by the CIBC at Delemont, Switzerland, and the CDA. The CDA released four species of insects during the 1970s; two tephritid flies (Urophora affinis and *U. quadrifasciata*) and a gelechiid moth (Metzneria paucipunctella) feed in the flower and seed heads and a buprestid beetle (Sphenoptera jugoslavica) bores in the stems. In the 1980s, the CDA also established a cochylid moth (Agapeta zoegana) and a weevil (Cyphocleonus achates) whose larvae feed in roots and stems, and a rust fungus (Puccinia jaceae) (Harris and Meyers 1984). Most of the insects now have been imported and released in the United States or have dispersed naturally into the country (Rosenthal et al., in press). Two other moths were released in the 1980s but did not become established: Pellochrista medullana in Canada and Pterolonche inspersa in the United States. The United States experimentally released a weevil (Bangasternus fausti) in Montana and Oregon in 1990 with state cooperation (Dunn and Campobasso 1990, Julien 1987). Additional promising insects are being tested by CIBC at Delemont and by ARS at Rome and Bozeman, Montana. A nematode. Subanguina picridis, from the USSR was established in Canada in 1976 to control Russian knapweed (Acroptilon repens) but has had little effect on the weed (Julien 1987). The combined effect of these control agents is beginning to reduce stands of knapweeds. As the recently established species increase and disperse, and as additional species are released and become established, control should increase substantially in both the United States and Canada.

Three European insect species were re-

leased by ARS in California from 1984 to 1988 for control of yellow starthistle (Centaurea solstitialis). These were a weevil (Bangasternus orientalis) and two tephritid flies (Urophora siruna-seva and Chaetorella australis) (Turner et al. 1990). Only the weevil is established in the field. Two other weevils (Eustenopus villosus and Larinus curtus) are being tested at Rome. All of these insects feed in the flower heads (Fornasari 1989). A European rust fungus (Puccinia jaceae) also is a good candidate for biological control of yellow starthistle (Bruckart 1989).

Seven additional species of insects have been introduced in Canada from 1963 to 1981 to control Canada thistle (*Cirsium arvense*), bull thistle, and sow thistle (*Sonchus arvensis*). Five insects are established in Canada and four in the United States, but to date, only slight control has been obtained (Kelleher and Hulme 1984, Julien 1987, Rees 1990). Additional insects and pathogens also are being tested in Europe, Canada, and Australia for these weeds (McClay 1990, Bruzzese et al. 1990).

Puncturevine (*Tribulus terrestris*) was substantially to completely controlled from California to Texas by two species of weevils of the genus *Microlarinus* (one, a seed feeder, and the other, a stem borer) from Italy that were released in 1961 (Andres 1978, Maddox 1981).

Tansy ragwort (Senecio jacobaea) has been substantially controlled in California, Oregon, Washington (Hawkes 1981), and British Columbia (Harris et al. 1984) by insects released by ARS and CDA. These are a foliage-feeding moth (Tyria jacobaeae) from Europe released in 1959 (it was previously tested in Australia in the 1930s but did not establish), a fleabeetle (Longitarsus jacobaeae) from Rome released in 1969 (Frick and Johnson 1973), and a leaf-mining fly (Pegohylemyia seneciella) from France released in 1966 (McEvoy 1985, McEvoy et al. 1990). Two additional European insects were released recently in Australia (Field 1990) and may be valuable in the United States as well. A rust pathogen also is under study in Europe.

By the 1970s, the toadflaxes (Linaria

vulgaris and L. dalmatica) were reduced, in most areas of Canada, from the status of serious weeds of rangelands and cereal crops (1950s) to weeds that were still common but caused little loss in yield. Two accidentally introduced insects, a flower-feeding beetle (Brachypterolus pulicarius) and a seed-feeding weevil (Gymnaetron antirrhinii), provided most of the control, with additional control coming in some areas from an intentionally introduced defoliating moth (Calophasia lunula). All species were from Europe (Harris 1984d).

European skeletonweed (Chondrilla juncea) has been introduced into rangelands and wheat fields in the Pacific Northwest. It became a serious pest in Australian wheat fields, but the worst of the three biotypes was almost completely controlled there by the 1970s by a rust (Puccinia chondrillina), with help from a mite (Eriophyes chondrillae) and a gall fly (Cystiphora schmidti), all introduced from Europe (Cullen 1978, Julien 1987). The mite and the gall fly, released in Washington in the 1970s, resulted in suppression of the weed, whereas the rust (released in 1976) only reduced plant vigor and not density (Piper 1985). In California, the rust provided most of the control (Supkoff et al. 1988).

A large project is underway at Bozeman, Montana and Regina, Saskatchewan to control poisonous European leafy spurge (Euphorbia esula) and the somewhat less damaging cypress spurge (E. cyparissias), which are rapidly invading rangelands in those areas. Since 1965, 13 species of European insects have been released in Canada or the United States: 7 of these are established in the United States and 4 are established in Canada (Harris 1984c; N. Rees, pers. comm. 1991). The first 12 were tested by the CIBC and were first released in Canada and later in the United States. A sphingid moth (Hyles euphorbiae) was released in 1966 but is ineffective because of heavy attack by ants and a virus. Two clear-winged moths were released in the 1970s — Chamaesphecia empiformis, which attacks only cypress spurge, and C. tenthrediniformis, which attacks leafy spurge - but neither established. Most of the releases have been made since 1982, when four species of flea beetles

in the genus Aphthona were released and established in Canada and, subsequently, in the United States: A. cyparissias, A. flava, A. nigriscutis, and A. czwalinae. Also, two species of anthomyiid flies were released in Canada (Pegomya euphorbiae and P. curticornie) and a gall midge (Spurgia esulae) was released in the United States, but only the latter is established to date (in Montana and North Dakota). Two other insects were released in Canada: a cerambycid stem borer (Obrerea erythrocephala) is established in Alberta and Montana, but the tortricid moth (Lobesia euphorbiana) is not yet established (Harris 1984c, Harris pers. comm. 1990, Julien 1987). In addition, the United States is testing (at Rome and at Bozeman) another clear-winged moth (Chamaesphecia crassicornis), a gall midge (Dasyneura sp. nr. capsula), a flea beetle (Aphthona abdominalis), and two noctuid moths (Symra dentinosa and Oxicesta geographica) (Pecora and Dunn 1990, Fornasari and Stazi 1990; N. Rees, pers. comm. 1991). A rust fungus (Melampsora euphorbiae) from Europe is also a promising control agent (Brukart et al. 1986). Recent explorations in northern China and Mongolia have revealed several additional species for possible introduction (Pemberton 1990).

The first evidence of control of leafy spurge is now being seen in Canada where several of the control agents have been established in the field for a few years. Apthona cyparissiae, A. flava, and A. nigriscutis have reduced leafy spurge reproduction or biomass more than 75% (but in less than 30% of the infested area). The latter species is particularly promising and is providing good control in open, well-drained prairies. Extensive redistributions of these insects are being made in the United States. As additional species are released and become established, control should improve substantially.

Limited research has been conducted by ARS since the 1950s to control five other weeds of western rangelands — gorse, Scotch broom (*Cytisus scoparius*), Mediterranean sage (*Salvia aethiopis*), Russian thistle (*Salsola australis*), and halogeton (*Halogeton glomeratus*) (Holloway 1964, Laing and Hamai 1976, Goeden 1978).

Only one or two insect species were released on each weed species and, to date, control has been negligible, although some of the insect species are now well-established (Julien 1987).

Weeds of Southwestern Rangelands

The most damaging weeds of rangelands in the southwestern United States and northern Mexico are native species that are either woody (brush) or poisonous herbs (Platt 1959, DeLoach 1981). These species have increased greatly during the last 150 years since the introduction of domestic livestock by the European settlers (Buffington and Herbel 1965). Several of the most damaging weeds have related species that are native in southern South America where they are attacked by guilds of insects and plant pathogens that also are native there. Several of these natural enemies are sufficiently host-specific that they could be introduced into North America. The biocontrol potential of these weeds is being investigated at ARS in Temple, Texas (DeLoach 1981, DeLoach et al. 1986). The first control agent, a root-boring weevil from Argentina, has now been released to control poisonous snakeweeds (Gutierrezia sarothrae and G. microcephala).

Saltcedars (primarily Tamarix chinensis and T. ramosissima) are the only introduced weeds that cause major damage to southwestern rangelands. Saltcedars are native to Asia and were introduced into the United States in the early 1800s as ornamentals. North America has no native species in the family Tamaricaceae. Athel (Tamarix aphylla), also introduced, is beneficial for the shade and windbreaks it provides; it is not a target for biocontrol. Saltcedar replaces the native vegetation; uses large amounts of groundwater that could be available for more beneficial plants and wildlife; increases soil salinity to a level where grasses and native shrubs cannot grow; and causes a narrowing and blockage of stream channels, thus increasing the risk of flooding. It has beneficial values as a nectar and pollen source for honeybees (it makes a poor-quality honey), it is good nesting habitat for the white-winged dove (but not for other doves), and it is used as a minor ornamental. Several phytophages on

saltcedar are known in Israel, Pakistan, and southern USSR that are excellent candidates for introduction (Horton and Campbell 1974, DeLoach 1990a).

African rue (*Peganum harmala*) is extremely poisonous to livestock and wildlife, although it is unpalatable. It was introduced from North Africa, probably in the early 1930s, and now occupies a few thousand acres centered on the commercial airports at Pecos, Texas and Demming, New Mexico and along highways leading from there. It could be a candidate for biological control but neither exploratory research nor testing have begun because it still occupies such a small area.

Northeastern Pasture Weeds

Batra (1981) listed 17 species of weeds, all introduced from Europe, that were under consideration by ARS as biocontrol targets in this area: hawkweeds (Hieracium vulgatum, H. florentinum, and H. aurantiacum), bedstraws (Galium aparine, G. verum, and G. mollugo), quickweeds (Galinsoga ciliata and G. parviflora), hempnettle (Galeopsis tetrahit), cinquefoils (Potentilla recta and P. norvegica), chickweeds (Stellaria media, S. graminea, and Cerastium vulgatum), henbit (Lamium amplexicaule), mayweed (Anthemis colula), and bindweed (Convolvulus arvensis). She also listed thistles (the genera Carduus, Cirsium, and Sonchus) and spurges (Euphorbia), which were being investigated primarily at other laboratories, and the aquatic Eurasian watermilfoil (Myriophyllum spicatum) as possible biocontrol targets. Batra surveyed the insects already present in the United States that attacked quickweeds, cinquefoils, and chickweeds. Research since the late 1960s at Virginia Polytechnic Institute and State University has concentrated on control of musk and other thistles, as discussed above, and preliminary work on other weeds has been initiated (Kok and Pienkowski 1985, Kok 1990).

Southeastern Aquatic Weeds

Research on biocontrol of aquatic weeds focused first on species that originated in South America, and later on some species from Eurasia and Australia. These weeds occur primarily from coastal North Carolina to eastern Texas; a few species occur in other areas of the United States (Andres and Bennett 1975, Brezonik and Fox 1975, Buckingham and Habeck 1990). The research was conducted by ARS at Gainesville and Ft. Lauderdale, Florida and at Stoneville, Mississippi (with strong support from the U.S. Army Corps of Engineers), and by the University of Florida at Gainesville (Coulson and Hagan 1985). Overseas research was done at the ARS Laboratory at Hurlingham, Argentina.

For control of alligatorweed (Alternanthera philoxeroides), three species were released in Florida: a flea beetle (Agasicles hygrophila) in 1964, a thrips (Amynothrips andersonii) in 1971, and a stem-boring pyralid moth (Vogtia malloi) in 1971 (Coulson 1977, Vogt et al. in press). Alligatorweed is no longer a pest, and chemical controls are no longer needed in most waters. However, the plant persists as the terrestrial form on the banks of streams or lakes and is sometimes a pest in rice fields in Mississippi and Arkansas (Center et al. 1990, Buckingham and Habeck 1990). A fourth insect, a flea beetle (Disonycha argentinensis) from Argentina, possibly could control the plant in these areas but uncertainties still exist regarding its host range (Cordo et al. 1984). Both A. hygrophila and V. malloi have given good control of alligatorweed in Australia, New Zealand, and Thailand (Julien 1987).

Waterhyacinth is probably the world's worst aquatic weed (Holm et al. 1977). It has spread from South America to nearly all tropical and subtropical areas. In the United States, it is a serious pest from South Carolina to Texas and in California. Many insects attack waterhyacinth in South America (DeLoach 1975, Perkins 1974). Three insect species were introduced from Argentina: two weevils (Neochetina eichhorniae in 1972 and N. bruchi in 1974) (DeLoach 1976), and a pyralid moth (Sameodes albigutallis) in 1977 (DeLoach and Cordo 1978, Center and Durden 1981, Center 1984). A mite (Orthogalumna terebrantis) entered the country by unknown means prior to 1968 (Cordo and DeLoach 1976). Heavy damage was inflicted to the plants, especially by N. eichhorniae, for ten years

after release before large-scale reduction in the plant populations was noticed. However, by 1985 the plant had been largely controlled at several release sites (Center and Durden 1986, Center et al. 1990). Acreage infested by waterhyacinth in Louisiana decreased from a peak of 729,000 ha in 1975 to less than 81,000 ha in 1984 (90% control), the result of damage inflicted by the introduced insects (Cofrancesco et al. 1985). Today, the weed remains a problem in a few areas, especially where herbicides are still used. Herbicides temporarily reduce plant biomass to a very low level, which causes populations of the control insects to crash. The plants then recover more rapidly than the insects and again become a pest (Wright and Center 1984). If the weed problem could be tolerated for two or three years in these areas until the insects could gain control, or if an integrated weed management program were developed, the need for herbicide application would be reduced or eliminated. Insects introduced by ARS have been requested and released in 13 other countries, where control also has been good to excellent (Julien 1987).

Hydrilla (Hydrilla verticillata) is a submergent aquatic plant that grows from as deep as 15 m. It escaped into Florida waters in the mid-1950s from aquaria. It now occurs to Texas and could spread throughout the entire United States and into Canada. It could become the worst aquatic weed in North America. North American hydrilla plants probably originated in southern Asia, although the species' native range extends into Australia and central Africa. Two species of insects from India were tested as hydrilla herbivores and released in Florida in 1987 — a tuber-feeding weevil (Bagous affinis) and a leaf-mining fly (Hydrellia pakistanae). Hydrellia n. sp. from northern Australia was released in 1989 (Center et al. 1990, Buckingham and Habeck 1990); additional insects from Australia are being

Waterlettuce (*Pistia stratiotes*) is also native to South America and the Old World tropics. It has become an increasingly serious pest in waters of the southeastern United States since alligatorweed and waterhyacinth were controlled. A tiny weevil

(Neohydronomus pulchellus) was tested in Argentina in the early 1970s (DeLoach et al. 1976) and was subsequently released in Australia in 1982 where it provided complete control of waterlettuce in tropical regions of the country (Harley et al. 1990). It was released in Florida in 1987 and by 1989 it had controlled waterlettuce at some release sites (Center et al. 1990, Buckingham and Habeck 1990).

The white amur fish or Chinese grass carp (Ctenopharyngodon idella) has been released in Arkansas, Florida, and Texas. It gives excellent control of hydrilla and other aquatic weeds but it also destroys nearly all other aquatic vegetation (Ware et al. 1975, Martyn et al. 1986). Methods have been perfected for producing sterile individuals or populations of only one sex. Populations of such fish possibly could be controlled to obtain a desirable balance of aquatic vegetation in a given body of water. The white amur is also an edible fish.

Several other introduced aquatic weeds such as Eurasian watermilfoil have been considered for biocontrol. The limited amount of exploratory research has not yet resulted in satisfactory control agents for these weeds. ARS scientists have experimentally controlled aquatic weeds of irrigation canals in California by planting a short, dense plant - spikerush (Eleocharis spp.) - that displaced the weeds but did not itself impede the flow of water (Yeo 1978). However, spikerush is difficult to establish under commercial usage of canals and has not come into widespread use. Biological control of certain species of algae has been investigated by European scientists (Brezonik and Fox 1975).

Weeds of Other Natural Areas

Most of the weeds of rangelands and aquatic sites discussed above could also be considered weeds of natural areas. Other weeds that have been introduced into natural areas cause loss of habitat for wildlife, are unsightly, compete with beneficial plants, or cause human health problems even though they are not agricultural pests. Some of these plants could be controlled by the introduction of foreign natural enemies if conflicts of interest could be resolved, or by

the augmentation of control agents already present.

Kudzu (Pueraria lobata) was introduced from eastern Asia by agricultural workers for erosion control and for livestock forage but has since spread along highways; it damages forest trees and is unsightly (Miller and Edwards 1983). Russian olive (Elaeagnus angustifolia) was introduced from Asia as an ornamental and as a windbreak but has become a serious weed in riparian areas of the southwest (Knopf and Olson 1984). Both of these probably could be controlled with natural enemies from their sites of origin if control were deemed desirable.

A tree (Melaleuca quinquenervia) from Australia, introduced into southern Florida as an ornamental, has escaped cultivation in recent years to become a very serious threat to the ecology of the Everglades. A recent cooperative project between ARS, CSIRO of Australia, and the U.S. National Park Service has already identified several promising insects for biocontrol (Center and Balciunas in press).

Purple loosestrife (Lythrum salicaria) is a semiaquatic weed that was introduced from Europe. It is a serious invader of wetlands in the northeastern United States and adjacent areas of Canada. It is spreading rapidly and has now reached Texas, California, British Columbia, and many areas in between. It has a disastrous impact on native vegetation, seriously reduces waterfowl and furbearer productivity, and further threatens several declining animal species (Thompson et al. 1987). Batra et al. (1986) found several promising control agents in Europe. Research is underway by ARS at Beltsville, Maryland to introduce these insects, which are being tested by the CIBC in Switzerland (Hight and Drea 1991).

Brazilian peppertree (Schinus terebinthe-folius) was introduced from Brazil into southern Florida as an ornamental and has become a serious weed of natural areas. Bennett et al. (1990), working at the University of Florida at Gainesville, found at least four insects in Brazil that are potential biocontrol agents. The introduced marijuana (Cannabis sativa) also could become

a candidate for biological control using insects that attack it in India (Batra 1976) or a fusarium wilt pathogen from Italy (McCain and Noviello 1985). Habeck (1990) determined that poison ivy (native to North America) possibly could be controlled in Bermuda using natural enemies from the United States. In North America, natural enemies from Asia might control the plant, if conflicts of interest regarding its usage as food by birds could be resolved.

Weeds of Cultivated Crops and Orchards

By far the greatest economic losses from weeds occur in cultivated crops (McWhorter and Chandler 1982, Chandler et al. 1984). While these areas are not considered natural areas, cultivated areas and many of the weeds that grow there are, nonetheless, important to wildlife, especially to birds. Also, some of these weed species extend into natural areas and their biological control (especially by the introduction of foreign control organisms) will have effects there. Crop weeds often have been considered difficult targets for biological control. Nevertheless, great success has been achieved in controlling a few of these weeds with pathogens and controls for others are under development (Ridings et al. 1978, Boyette and Walker 1985, Phatak et al. 1987, Boyette 1988, Charudattan and DeLoach 1988, DeLoach 1990b).

FUTURE TRENDS IN THE BIOLOGICAL CONTROL OF WEEDS

In rangelands, aquatic sites, and natural areas, biological control of those weeds for which appropriate control agents can be found is nearly always the most ecologically sound method. Biological control by the introductory approach is nearly always the most economical method. Biocontrol by the augmentative approach may be more or less expensive than other methods; however, even when it is more expensive it may be the method of choice when the ecological cost or risk to human health (from using chemical or mechanical controls) is high.

In the past, most weeds have been successfully controlled by only one or two control agents; examples are prickly pear cacti, St. Johnswort, musk thistle, waterhyacinth,

alligatorweed, waterlettuce, puncturevine, and tansy ragwort. Others (such as lantana) have required the combined effect of several control agents. Several weeds presently under investigation, such as leafy spurge, knapweeds, saltcedar, melaleuca, and hydrilla, appear to be in the latter category. Some past projects that were written off as failures still might succeed if additional organisms are introduced. Some weeds apparently have only a few species of control agents within their natural distribution that are suitable for introduction, while others have many.

Some past failures may have resulted because the best source of control agents was politically inaccessible. Control agents may now be found in the USSR and China that will control leafy spurge, halogeton, Russian thistle, and other weeds. However, foreign biocontrol agents probably do not exist that are sufficiently damaging and sufficiently host-specific to control every introduced weed of importance.

Great promise lies in the development of augmentative approaches to biocontrol, especially for weeds in cultivated crops or home lawns and gardens, and especially by using plant pathogens. Several very promising plant pathogens have been found that have the potential to control some of the most damaging crop weeds. Further developments, such as the use of invert emulsions or other innovative formulations that allow consistent infection under the variable microclimate in the field, could lead to effective biocontrols. Genetic engineering could modify a pathogen to obtain consistent infection and disease development.

Imaginative methods of integrating biological control with herbicidal, mechanical, or cultural controls could provide for vastly more effective weed management in all agro-ecosystems. The timing of cultivation or pesticide applications, crop rotation, the maintenance of reservoirs for the biocontrol agent, and crop residue management have already allowed the development of highly effective management systems for several insect pests; similar systems could be effective in weed control.

In the past, unresolved conflicts between

the damage caused by weeds and their various beneficial values have prevented attempts to control weeds that potentially could be controlled. Such conflicts probably will be of even greater concern in the future as environmental health is balanced against agricultural production. Improved methods of analysis and comparison can reveal control approaches that will allow for the greatest overall benefit. The future probably will see a much greater emphasis on ecological and economic analyses in the selection of weeds as targets for attempted biological control.

In past project planning, biological control of native weeds was often considered either too difficult or too dangerous to risk scarce research funds on an introductory approach to control. Recent ecological analyses have shown that if proper precautions are taken, the risks to the ecosystem are not great. The currently recognized non-equilibrium paradigm of terrestrial ecosystems (Ecological Society of America 1990) does not predict ecosystem collapse when an overabundant native species is substantially reduced in density. If the native weed has close relatives on other continents, effective natural enemies may exist there that will attack the weed and that are sufficiently host-specific not to attack beneficial plants.

In the future, user and public education will have a greater influence on the development of effective weed management systems. Complete eradication of a weed is not necessary if a biocontrol agent capable of suppressing weed outbreaks remains always present. In rangelands and other natural ecosystems, the stress on a weed produced by competition from other plants, after partial control by introduced insects has been achieved, often contributes to satisfactory control. The determination of economic or ecological thresholds of weed damage at different times during the growing season may allow a partially effective biocontrol agent to contribute significantly to an effective weed management system. In aquatic habitats, the patience of waterfront property owners and pesticide applicators, to tolerate the weed for two or three years until a control agent can gain the upper hand, would reduce or eliminate the need for chemical controls of some weeds.

Both ecological theory and experience support the thesis that biocontrol should be the first approach tried in many situations. In the past, biological control was often regarded as an alternative only when all other means of control failed. A more rational approach is to examine the more damaging weeds of a given ecosystem to determine which have the best potential for biological control by optimizing three factors: (1) greatest reduction in damage caused by the weed, (2) least harm to beneficial values of the weed if it is controlled, and (3) greatest chances of finding host-specific and successful control agents.

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