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A case for using insects as control agents, after rigorous screening, and for integrating release strategies with research

Richard A. Malecki, Bernd Blossey, Stephen D. Hight, Dieter Schroeder, Loke T. Kok, and Jack R. Coulson

Purple loosestrife (*Lythrum salicaria* L.) is an exotic wetland perennial responsible for the degradation of many prime wetland habitats throughout the temperate regions of the United States and Canada. Large, monotypic stands reduce the biotic diversity of wetland systems by replacing native plant species (Stuckey 1980) and thereby eliminating the natural foods and cover essential to many wetland wildlife inhabitants, including waterfowl (Friesen 1966, Rawinski and Malecki 1984, Smith 1964). In North America, this plant is a classic example of an introduced species whose distribution and spread has been enhanced by the absence of natural enemies and the disturbance of natural systems, primarily by human activity. Although noted for the beauty of its late summer inflorescence, which also provides a nectar and pollen source for bees, loosestrife has few other redeeming qualities and is listed as a noxious weed in 13 states, where its importation and distribution is prohibited.

Current efforts to control purple loosestrife center on importation of host-specific phytophagous insects from the plant's native range in Europe, a practice applied in North America since the late 1880s (Dahlsten 1986) and based on ecological theory of biological invasions. However, with few exceptions, general acceptance of biological methodologies in the practice of modern weed management have not been well endorsed or financially supported (Tauber and Baker 1988). Skepticism concerning the safety and effectiveness of exotic insect introductions for weed control remains prevalent among the general public, administrators, and even scientists. A shortage of highly visible, successful introductions over broad portions of the continent, coupled with a general lack of studies to adequately monitor the impact of planned releases on host plants and nontarget species, have contributed to this skepticism.

Controlled manipulations offer opportunities for increased understanding of the ecology and genetics of plant-insect interactions

Our program for the biological control of purple loosestrife is intended to reverse the massive degradation of wetland habitats currently attributed to encroachment by this species. It is also intended to demonstrate the rigorous protocol required by the US Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) for screening foreign insects before their release into the United States and to emphasize the need for postrelease monitoring and research investigations. Controlled manipulations of insects and plants proposed for this program offer opportunities for increased understanding of the ecology and genetics of invasions, plant-insect interactions on target and nontarget species, and factors controlling reestablishment of native vegetation.

North American invasion pattern

Invasion of North American wetlands by *L. salicaria* began in the early nineteenth century, when the plant was introduced both as a contaminant of European ship ballast and as a valued medicinal herb for treatment of diarrhea, dysentery, bleeding, wounds, ulcers, and sores (Stuckey 1980). By the 1830s, purple loosestrife was well established along the New England seaboard. The construction of inland canals and waterways in the 1880s favored the expansion of the plant into interior New York and the St. Lawrence River Valley (Thomp-

Richard A. Malecki is a wildlife research biologist with the US Fish and Wildlife Service's New York Cooperative Fish and Wildlife Research Unit, Cornell University, Ithaca, NY 14853. Bernd Blossey is a visiting scientist from Germany currently affiliated with the New York Cooperative Fish and Wildlife Research Unit at Cornell. Stephen D. Hight is an entomologist/botanist with the US Department of Agriculture's Agricultural Research Service, Insect Biocontrol Laboratory, Beltsville, MD 20705. Dieter Schroeder is an entomologist with the CAB International Institute of Biological Control, Delemont, Switzerland. Loke T. Kok is a professor in the Department of Entomology and head of the Beneficial Insect Quarantine Laboratory at Virginia Polytechnic Institute and State University, Blacksburg, VA 24061. Jack R. Coulson is an entomologist with USDA's Insect Biocontrol Laboratory in Beltsville, MD 20705.

son et al. 1987). The continued expansion of *L. salicaria* coincided with increased development and use of road systems (Thompson et al. 1987), commercial distribution of the plant for horticultural purposes, and regional propagation of seed for bee forage (Pellet 1977).

The plant now occurs in dense stands throughout the northeastern United States, southeastern Canada, the Midwest, and in scattered locations in the western United States and southwestern Canada. Newly created irrigation systems in many western states have supported further establishment and spread of *L. salicaria*.

Plant characteristics

A variety of characteristics exhibited by *L. salicaria* have enabled it to become a problem in North America. A single, mature plant can produce more than 2.5 million seeds annually. These seeds are long-lived (Welling and Becker 1990) and easily dispersed by water and in mud adhering to aquatic wildlife, livestock, and people (Thompson et al. 1987). Under natural conditions, seedling densities can approach 10,000–20,000 plants/m^2 with growth rates exceeding 1 cm/day (Rawinski 1982). Competition from seedlings of other plant species on newly exposed sites is minimal.

Established plants are tall (approximately 2 m), with 30–50 stems forming wide-topped crowns that dominate the herbaceous canopy. A strong rootstock serves as a storage organ, providing resources for growth in spring and regrowth if the aboveground shoots are cut, burned, or killed by application of foliar herbicides. Such attributes allow it to outcompete and even eliminate other plant species in both natural and managed wetland habitats. No native herbivores or pathogens in North America are known to suppress it (Hight 1990). Historically, multiple introductions of *L. salicaria* into North America and the absence of specialized herbivores may have changed its genetic heritage and contributed to its competitiveness.

Current problem

Invasion of purple loosestrife into a wetland system results in suppression of the resident plant community and the eventual alteration of the wetland's structure and function (Thompson et al. 1987). Large monotypic stands of *L. salicaria* jeopardize various threatened and endangered native wetland plants and wildlife, such as a local bulrush (*Scirpus longii* Fern.) in Massachusetts (Coddington and Field 1978), dwarf spike rush (*Eleocharis parvula* Rom and J. A. Schultes) in New York (Rawinski 1982), and the bog turtle (*Clemmys muhlenbergi* Schoepff) in the northeastern United States (Thompson et al. 1987).

The invasion of *L. salicaria* into North America has also caused agricultural losses. Reduction of wetland pasture and hay meadows is attributed to the plant being less palatable to livestock than are native grasses and sedges (Thompson et al. 1987). Heavily infested sites are difficult to mow and manage. In western states, the establishment of *L. salicaria* in irrigation systems has impeded the flow of water and generated substantial concern.

No effective method is available to control *L. salicaria*, except where it occurs in small localized stands and can be intensively managed. In such isolated areas, uprooting the plant by hand and ensuring the removal of all vegetative parts can eliminate *L. salicaria*. Other control techniques that have been used include water-level manipulation, mowing or cutting, burning, and herbicide application (Malecki and Rawinski 1985, McKeon 1959, Smith 1964). Although these controls can eliminate small and young stands, they are costly, require continued long-term maintenance, and, in the case of herbicides, are nonselective and environmentally degrading.

The case for biological control

Biological control of weeds is the human manipulation of a plant's natural enemies to reduce populations of the plant pest to an acceptable level. In nature, natural enemies, as well as competition with other plants, prevent many plants from expanding their distribution. In turn, the abundance of the plant (acting as a host) often influences the abundance of the natural enemies. Ideally, these interactions provide a self-sustaining, balanced system. An objective of our project is to find and manipulate the most effective natural enemies for control of *L. salicaria*.

Biological weed control in North America received prominent recognition in the 1950s with the successful introduction of two leaf beetles to control the European range weed, St. Johnswort or Klamath weed (*Hypericum perforatum* L.; Huffaker and Kennett 1959). The success of this classic control effort and others that followed (e.g., alligatorweed, *Alternanthera philoxeroides* Mart., Coulson 1977; muskthistle, *Carduus thoermeri* Weinmann, Kok 1986, Kok and Surles 1975; and ragwort, *Senecio jacobaea* L., McEvoy et al. 1991) have demonstrated that with judicious research and testing procedures, long-lasting, cost-effective, environmentally sound, and effective control programs can be implemented for a variety of troublesome plant species. Success in such programs has greatly reduced the dependence on chemical control of these weeds. No introduced insect agents has ever exterminated either the target weed or a desirable plant (Harris 1988), nor have they ever switched hosts to become serious pests of crop plants (Crawley 1989).

Biological control of *L. salicaria* has great potential in North America. Other introduced weeds that have been successfully suppressed by biotic agents share similar attributes. These attributes include status as an introduced perennial, the existence of several effective natural enemies in its native region, restriction to a specific and relatively stable habitat, a fairly continuous distribution, taxonomic isolation from economically valuable plants, and the occurrence of unfilled feeding niches for exploitation by natural enemies.

Surveys and screening. Biological attributes of insect herbivores, such as their host specificity, host-searching ability, fecundity, larval survival, and dispersal, have long served as guidelines for selection of biological control agents (Goeden 1983, Harris 1973, Huffaker et al. 1977). However, such characteristics are not easily isolated or observed in the field (Ehler 1990), and those that distinguish successful agents from unsuccessful ones are not easily defined (Crawley 1986, 1989, Roush 1990).

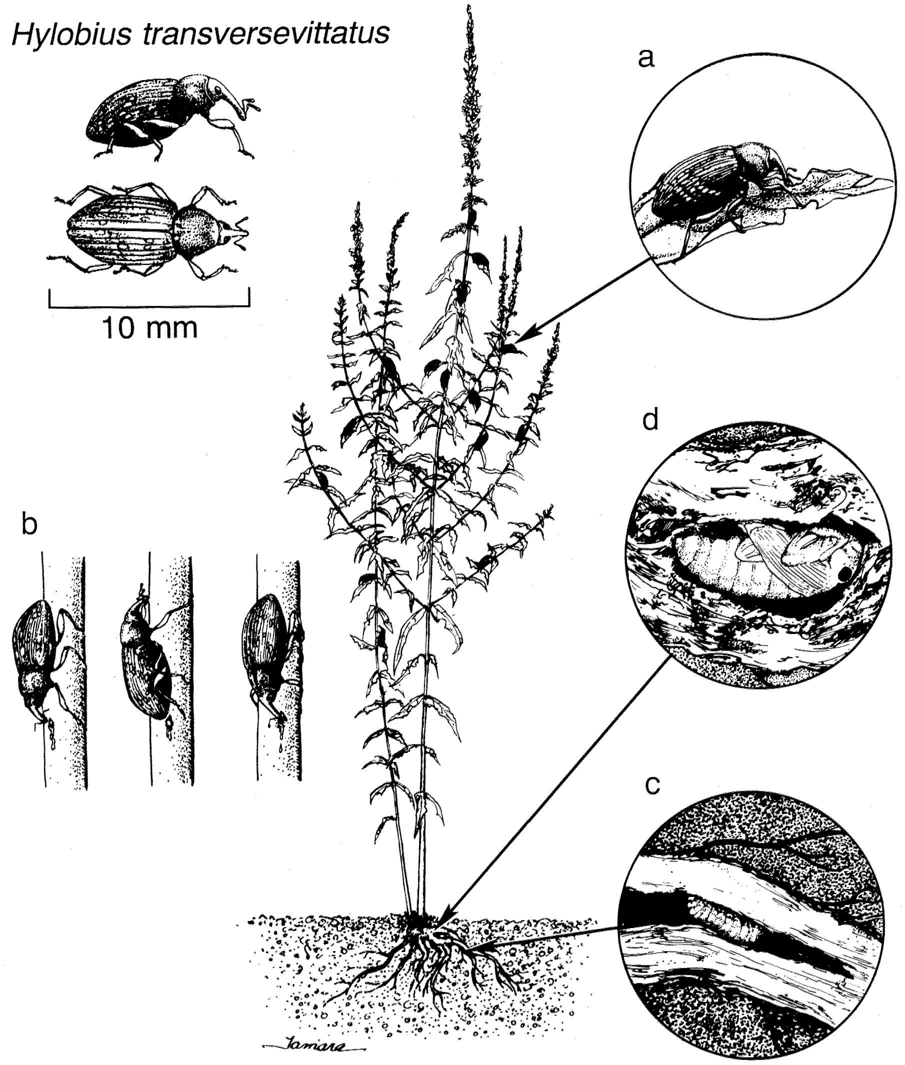

Figure 1. Life cycle of *Hylobius transversovittatus*. **a.** Adults emerge in spring and feed nocturnally on newly formed leaves of *Lythrum salicaria*. **b.** Oviposition lasts two to three months and consists of one to three eggs individually deposited each day into the stem and covered with frass. **c.** Developing larvae mine to the roots, where they feed extensively on root tissue. **d.** Mature larvae form a pupation chamber in the upper part of the root, emerging as adults in late summer or the following spring. Adults may live for several years.

In 1987, Thompson and colleagues completed a detailed review of the taxonomy of *L. salicaria*, its distribution, biology, ecology, economic value, and control in North America. While the review was in progress, scientists in Europe, where *L. salicaria* originated, were searching for potential natural enemies (control agents). That work was conducted in association with the USDA Agricultural Research Service (ARS) and the US Fish and Wildlife Service (USFWS; Batra et al. 1986, Blossey and Schroeder 1986). The initial success of the interagency effort led to the formation of a scientific advisory group with additional representation from Canada, other US federal agencies, and universities. This working group provided continual guidance on all aspects of our biological control program.

Of 120 species of phytophagous insects associated with purple loosestrife in Europe, 14 species were considered host-specific to the target plant. From this group, six species were selected as the most promising for biological control. These species were a root-mining weevil, *Hylobius transversovittatus* Goeze (Figure 1), which attacks the main storage tissue of *L. salicaria*; two leaf-eating beetles, *Galerucella calmariensis* L. and *Galerucella pusilla* Duftschmid (Figure 2), which are capable of completely defoliating the plant; two flower-feeding beetles, *Nanophyes marmoratus* Goeze and *Nanophyes brevis* Boheman, which severely reduce seed production; and a gall midge, *Bayeriola salicariae* Kieffer (Gagné 1991), which similarly reduces seed production by attacking the flower buds. Five of these species are found throughout the range of *L. salicaria* in Europe, even on small isolated stands, so they have an excellent colonizing capacity. The sixth, *N. brevis*, is restricted to southern Europe.

To investigate the effect of these insect species on the performance of the host plant, field populations of *L. salicaria* in Europe were observed for several years. Plant recruitment, winter survival, growth, flowering period, seed output, and insect attack were recorded (Blossey 1991). Such studies are often missing in biological weed control programs, but they are necessary to understand the ecological interactions of host plants and insect herbivores (Crawley 1989). These studies improve the basis for selection of successful candidate species. At the same time, detailed studies of the taxonomy, distribution, and life history of *H. transversovittatus*, *G. calmariensis*, and *G. pusilla* were also being conducted (Blossey 1991).

The broad geographic distribution of the root-mining weevil and two leaf-feeding beetles and their dramatic effect on the growth and vigor of purple loosestrife were the primary reasons for selecting them for the initial phase of natural enemy introductions into the United States. To assure that other plant species are not at risk, a test plant list of approximately 50 species was compiled for each insect species. These test plants included plants that are taxonomically related to purple loosestrife or are considered of ecological or economic importance. Testing was done at the International Institute of Biological Control in Europe (Blossey and Schroeder 1991) and under quarantine conditions in the United States (Kok 1992, Kok et al. 1992). The host-specificity tests of the three insects examined not only their ability to feed and survive on a particular plant species but also to complete an entire life cycle.

Results from our plant tests identified two native North American plants as potential hosts for the insects proposed for release: *Decodon verticillatus* L., Ell. (commonly known as swamp loosestrife or waterwillow) and *Lythrum alatum* Pursh (winged loosestrife), both of the family Lythraceae and closely related to *L. salicaria*. Concerns for these species prompted further investigation in Europe, where potted plants were exposed to natural populations of the insects to examine their susceptibility under field conditions. The results showed that, if given a choice, all three insect species avoided the two native American plants (Blossey and Schroeder 1991, Malecki et al. 1991). In the meantime, screening of *N. brevis*, *N. marmoratus*, and *B. salicariae* was successfully completed in Europe (Blossey and Schroeder 1992), thus keeping these insects on our active list of potential control agents.

All survey and screening studies to import into the United States *H. transversovittatus* and the two *Galerucella* species were reviewed by the Technical Advisory Group on the Introduction of Biological Control Agents for Weeds (Coulson and Soper 1989). This select group of weed biocontrol experts from throughout the United States provide direct consultation to USDA-APHIS. A similar review was conducted in Canada. Final approval from APHIS, in conjunction with appropriate state regulatory agencies, was required before importation and release of the three insects.

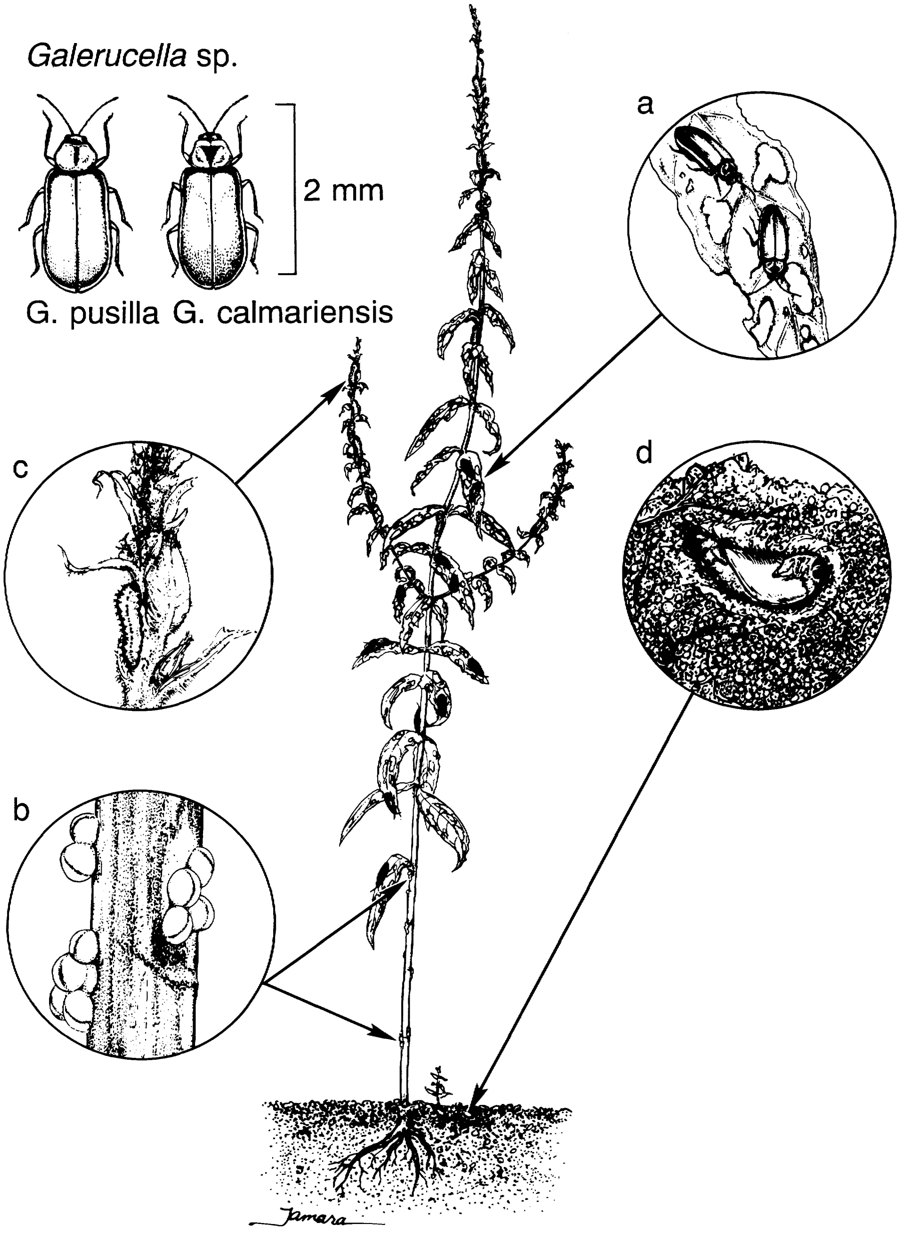

Figure 2. Life cycle of *Galerucella calmariensis* and *Galerucella pusilla*. **a.** Adults emerge in spring and feed on newly formed leaf tissue of *Lythrum salicaria*. **b.** Spring oviposition lasts approximately two months; batches of two to ten eggs are laid daily on the plant stem or in leaf axils. **c.** Developing larvae feed extensively on bud, leaf, and stem tissue. **d.** Pupation to adult occurs in the soil or litter near the host plant. Adults are short-lived, dying soon after the spring oviposition period.

Propagation and release. No consistent methodology is available for the deliberate introduction of insects into new environments. A primary consideration in the establishment of insect control agents is their ability to adapt either climatically or genetically to their surroundings. DeBach and Bartlett (1964) noted that failure of insects to adapt to new climates is the major cause of unsuccessful colonization. Beirne (1975) reasoned that the greater the number of individuals released at a site, the greater the genetic diversity of the colony and its inherent ability to produce the necessary genetic combinations to thrive in new surroundings. Likewise, the more insects the greater is the probability of individuals finding hosts and mates sufficient to enable the population to survive. Other considerations noted by Beirne include the physical characteristics of release sites with respect to meeting the essential needs of introduced agents and preventing dispersal loss before colonization and the synchrony and taxonomic compatibility of the predator species and their host. All factors have a potential role in the degree of success achieved.

Predation of the two *Galerucella* species by spiders was evident at all field sites in Europe. Larvae were attacked by *Asecodes mento* Walk. (Eulophidae) and adult beetles by *Centistes rufithorax* Telenga (Braconidae), two parasitic wasps. As a prerelease precaution, studies of a closely related beetle, *Galerucella* *nymphaeae* L., occasionally found in association with *L. salicaria* in the northeastern United States, were conducted to identify potential sources of mortality that might negatively affect colonization at release sites. No parasites or pathogens were detected, but large numbers of eggs were consumed at our field sites by ladybird beetles, *Coleomegilla maculata*.[1] Developmental and reproductive requirements of the *Galerucella* species were also studied. Mass rearing of these species in the laboratory could become necessary to supplement numbers available for field release or to use in timed releases of insects that correspond with optimal survival periods.

In June 1992, *H. transversovittatus*, *G. calmariensis*, and *G. pusilla* were approved by USDA-APHIS for introduction into the United States. Field collections of the three species, reared under laboratory conditions in Europe and screened under quarantine, provided insects that were free of parasitoids and diseases. The insects were released in New York, Pennsylvania, Maryland, Virginia, Minnesota, Oregon, and Washington state. Stocks of the three beetles were also sent to Canada, where their release was also approved.

Historically, introduction strategies for biological control agents have ranged from single-species releases to what Ehler (1990) describes as the empirical approach, "in which one simply releases all suitable natural enemies which happen to be available, with the hope that the proper species or combination of species will be sorted out in the field" (p. 113). With *L. salicaria*, our strategy is to achieve long-term control through provision of a simple, yet diverse, collection of natural enemies. Through evaluation of single- and multiple-species releases, we hope to refine current methodologies for selecting natural enemies for the biological control of perennial weeds.

Propagation of insects in the United States requires establishment of field nurseries at select sites where larvae and/or adults can be reared for fall release or overwintered for release or continued propagation the following spring. We plan to release insects that originate from major rearing centers located in the northeast, midwest, and northwest regions of the United States. Details pertaining to numbers of insects to be released, location of release sites, time of releases, use of multiple- versus single-species releases, and so on, are still being developed.

Merging traditional release strategies with research

Not all releases of biological control agents are successful, and control is not always achieved even when agents are successfully established. The lack of follow-up studies after the release of insect control agents makes it difficult to understand why certain introductions fail whereas the same agents succeed in other areas (Crawley 1989). A better understanding is needed of how such basic mechanisms as colonization and dispersal of insect agents, released into new environments with variable climatic conditions and spatial distributions of the host plant, influence the stabilization and function of a biological control program.

Most plant species are associated with a variety of phytophagous insects within their native range. Such groups of insect species constitute ecological communities whose structure and population dynamics are strongly influenced by habitat, topography, and the distribution and abundance of their host plants. Therefore, the ability to identify those species and their attributes having the greatest potential impact on the host plant requires an understanding of community interaction at all three trophic levels: the plant, its insect associates, and their natural enemies.

Efforts to duplicate or restructure all or part of a natural insect herbivore community, outside the home range of the host plant, represent an exercise in ecological theory that is often founded on poorly developed or tested hypotheses (Waage 1990). A diverse array of natural enemies is reduced to but a few species for pre-introduction studies, quarantine, and release. The basis for selection of these agents involves decisions that begin at the time of exploration and continue through the prioritization of agents on the basis of their host specificity and likely efficacy. Unfortunately, we are far from being predictive about the potential of host-specific herbivores to control a particular plant (Crawley 1989).

Our 1992 insect releases occurred in climatically different regions across North America. At the same time, we started experiments to determine the critical number of individuals needed for release and the time of year best suited for their successful establishment. Experiments with genetically different insect populations are being conducted to investigate the influence of genetic diversity on colonization. We also plan to release agents in a variety of combinations to evaluate the effectiveness of single- and multiple-species herbivory on the host plant.

Predictions

The following predictions emerge from what we have learned about the interaction of purple loosestrife and its specialized herbivores:

- All species introduced or proposed for introduction will become established throughout the current range of purple loosestrife in North America. Our findings to date indicate that the two *Galerucella* species successfully overwintered and started oviposition at all release sites. The most difficult species to establish will be *H. transversovittatus*, because of its long life cycle and low fecundity. However, we predict that once high numbers are achieved in the field, all species will spread rapidly. Insects are likely to have difficulty finding the scattered populations of purple loosestrife in the arid Midwest and the Pacific Northwest, so redistribution of agents to new infestations might be necessary.

- Three species, *H. transversovittatus*, *G. pusilla*, and *G. calmariensis*, will be most important for the control of purple loosestrife. Defoliation by the chrysomelids will be more spectacular, but the devastation of the rootstock by weevil larvae will have a long-term negative impact on plant performance. The flower-feeding weevils, *N. brevis* and *N. marmoratus*, will stabilize reduced levels of the plant population by further reducing the seed output such that not every disturbance in a wetland will lead to

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[1] M. Tauber and C. Tauber, 1993, Cornell University, Ithaca, NY. Personal communication.

an outbreak of *L. salicaria.*

- Combinations of insect control agents will have a greater effect on plant performance than will any species alone. Purple loosestrife populations will also be more easily controlled in the southern part of its current range because the shorter generation time of insects there allows them to increase more rapidly.
- Control of purple loosestrife will be achieved more rapidly in mixed plant communities where competition for space and nutrients is greater.
- In general, we predict a reduction of purple loosestrife abundance to approximately 10% of its current level over approximately 90% of its range. Plant refugia will remain at sites with high water levels that prevent development of the root-mining weevil and limit recruitment of the *Galerucella* species. Plants growing in the shade will also be less likely to be attacked by the control agents. In wetlands with an existing soil seed bank of *L. salicaria*, new disturbances will result in reestablishment of the plant for many years. However, these new populations will be colonized by the control agents, and mixed vegetation will replace the monotypic stands.

Conclusions

The application of biological weed control as an alternative or complement to the use of chemical herbicides continues to be poorly promoted or endorsed in the United States and other countries. Basic research involving the biology, demographics, and ecological interactions of both host-plant species and the insect agents being used to control them is lacking. Consequently, despite an increase in the number of control programs initiated in the past decade, the ability to select and establish potential control agents has not progressed to a point where the rate of success has improved (Crawley 1989).

Our program for the biological control of purple loosestrife focuses on an international environmental weed problem that cannot be controlled by conventional means. With support from federal and state agencies, we have brought together an international scientific advisory staff whose goal not only is to participate in and oversee the selection, screening, and introduction of an insect predator community to provide a long-lasting biological control mechanism for loosestrife, but also to develop a corresponding program of research and evaluation useful to the enhancement of future programs in this area. Only through increased visibility and credibility as a predictive science with proven implementation procedures based on rigorous experimental tests can we hope to integrate more successfully the practice of biological weed control into national and international efforts aimed at integrated pest management.

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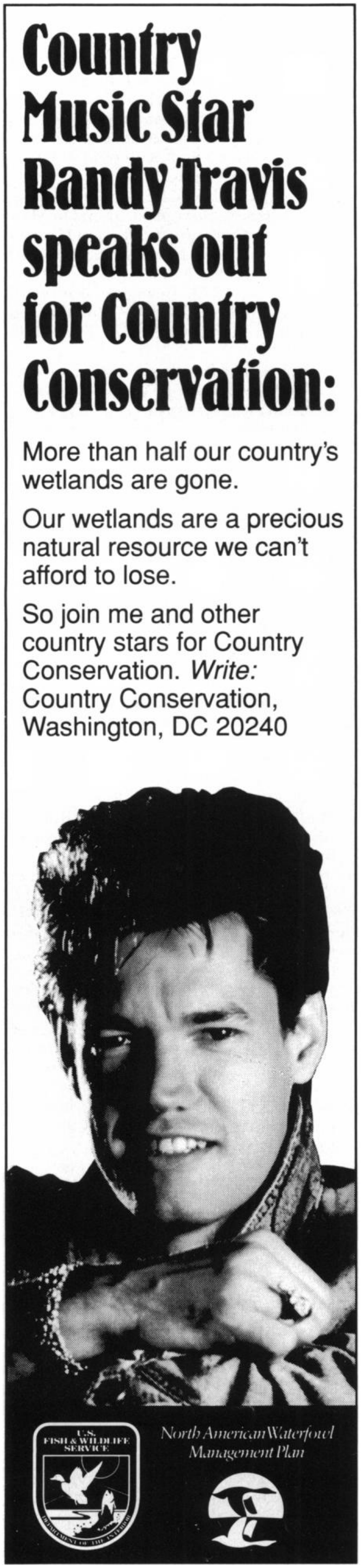

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