

SETTING PRIORITIES FOR THE BIOLOGICAL CONTROL OF WEEDS: WHAT TO DO AND HOW TO DO IT

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Abstract. Three options are available for dealing with non-indigenous plant species that either may become or already have become invasive weeds; keep them out, eradicate introduced populations while they are still small, or finally attempt biological control of established populations. By far the best approach to controlling potentially invasive foreign weeds is to limit the introduction of plants to new areas. Better communication of the consequences and environmental costs of these species may help balance the pressure applied on regulatory agencies by industries to permit commercial plant importations under few limitations. Eradication attempts must be bold and fast. Proponents of the program should not make unrealistic promises because eradication is so difficult to achieve. Finally, biological control does have a potential role in the management of non-indigenous weeds. However, finding agents that are capable of reducing the densities of plants is not an easy task. Successful biological control agents are capable of killing or greatly reducing the vigor of their host plants at life stages for which little compensation can occur. Greater focus on efficacy can help reduce the number of non-indigenous species that are introduced in biological control programs.

Keywords: eradication, invasive plants, seed predators, plant introductions, quarantine, noxious weeds

INTRODUCTION

Over the last 500 years transoceanic travel and commerce has led to a global redistribution of non-native plants (Moody and Mack 1988). Without natural enemies, many alien plants have established, invaded and displaced native vegetation (Mack *et al.* 2000). Three options are available for dealing with alien plant species that either may become or already have become invasive weeds; keep them out, eradicate introduced populations while they are still small, or finally attempt biological control of established populations.

PRIORITY ONE - KEEP THEM OUT

Although exclusion is the most effective way to prevent potentially invasive weeds, regulations to stop the introduction of weeds has been woefully ineffective. In the USA at least 2000 non-native plants are invading managed and natural systems. This includes at least 235 woody plants and 600 herbaceous plants, including grasses and aquatic species (Reichard and Campbell 1996). A majority of non-indigenous weeds were introduced intentionally to areas where they were not native and where they have become serious environmental or agricultural pests. In the USA 85% of the 235 species of woody plant invaders were introduced as ornamentals or for landscaping (Reichard and Campbell 1996). In Australia approximately 46% of noxious weeds have been introduced for ornamental or other purposes (Panetta 1993). In the city of Zurich alone 300 plant species have naturalized, 52% for ornamental purposes, and these are

thought to have led to the disappearance of more than 150 native species (Landolt 1993).

It is not surprising that the types of plants valued by horticulturalists are also those with characteristics that preadapt them to be weeds. Species favored by horticulturalists plants are those that produce many flowers, begin to flower early in the season, are easy to propagate, and that grow well in disturbed sites (White and Schwarz 1998). The prevention of weed introductions therefore creates a tension between agencies regulating plant introductions and the horticultural and agricultural industries. In Australia the government restricts the entry of plants via the Quarantine Act of 1908 that prohibits taxa from 19 genera and 66 species (Panetta 1993). However, plants being introduced by nurseries and the gardening industry are not included on these schedules.

Given the pressure by commercial ventures to introduce foreign plants, and the need for quarantine regulations to protect against invasive weeds, a procedure for predicting the potential invasiveness of non-indigenous plants is required. Schemes for assessing plant species prior to introduction have been proposed by Panetta (1993), Reichard and Hamilton (1996), and White and Schwarz (1998). White and Schwarz (1998) compare the traits of plants desired by gardeners and those of invasive weeds. They list the following traits to be in common; rapid growth, early and many flowers, prolific seed production, good seed germination, and no major pests. Adaptations for efficient dispersal and vegetative spread are also likely to apply to both situations. Reichard and Campbell (1996) developed a scheme for predicting the invasiveness of plants by comparing the traits of 235 species of plants known to be invaders to those of 87 noninvasive plants. These comparisons were based on plant growth rates, juvenile periods, germination requirements and the ability to reproduce vegetatively. Under this system plants can be categorized into those to be rejected, accepted or held for further examination. White and Schwarz (1998) tested the ability of Reichard's scheme to predict the invasiveness of known plant invaders and found that 85% would have been rejected by the scheme, 13% would have been held for further examination and 2% would have been accepted.

Panetta (1993) proposed a scheme based on earlier work of (Hazard 1988). He assigned a point value to different characteristics; plants receiving a value of twenty or more points are rejected while those with a value of 12 or less are accepted, and those in-between are further investigated (Table 1). This system rejects outright aquatic plants, potentially causing friction with the major industry selling aquatic plants for aquaria and ponds.

Another system for evaluating the invasiveness of plants is the Australian weed risk assessment scheme proposed by Pheloung (1995 cited in White and Schwarz 1998). This system relies on a number of plant attributes including whether the plant is a known invader, as well as other biological characteristics having to do with climatic requirements, reproduction, dispersal, persistence, noxiousness, and distribution. Invasiveness elsewhere is also considered. Overall there are 49 questions divided into 8 categories. Nonweedy traits receive a score of 0 or -1, unknown traits a score of 0, and weedy traits a score of 1. Some scores are weighted differently depending on the answer to the question. Plants receiving a score of 0 or less are considered safe for introduction while those with a score greater than 7 are considered to be potentially weedy invasives. This system focuses on vegetative growth and the ability of plants to tolerate a range of conditions and high levels of damage. It also includes characteristics such as the possession of parasites, toxicity and the seed type produced.

White and Schwarz (1998) tested the ability of this system to reject plant species already known to be invasive in Australia and of the current invaders, 84% would be rejected by this scheme, 16% fell into the category of requiring future study and none would have been accepted. More recent versions have questions dealing with dispersal attributes.

Criterion	Point value
Is the species free-floating aquatic or can it survive and reproduce as a free-floating aquatic	20
Is it a weed elsewhere	20
Are there close relatives with a history of invasion to similar habitats	10
Is it spiny	10
Are diaspores spiny	10
Is the species harmful to animals	8
Does the plant produce stolons	5
Does the plant reproduce vegetatively	8
Are diaspores wind-dispersed	8
Are diaspores dispersed by mammals or machinery	8
Are diaspores dispersed by water	5
Are diaspores dispersed by birds	5

Table 1. Evaluation scheme proposed by Panetta (1993) to predict potential invasiveness of plants.

These evaluation schemes may not be perfect but they do suggest criteria that could be used effectively to slow the continued introduction of potentially invasive plants. There is a great need to apply political pressure to tighten regulations on the purposeful introduction of plants. Currently the interests of the nursery and ornamental plant industry are served with little regard for the environmental impacts of invasive, non-indigenous species. Greater publicity on the cost of these weeds, and better education of landscape architects, plant breeders, home and commercial gardeners, pet store owners and those with aquaria and garden ponds are a necessity.

PRIORITY TWO - ERADICATION

Following the introduction and establishment of a non-indigenous plant there may be a short time-window in which the species might be eradicated (Myers *et al.* 2000). Eradication is particularly difficult for plants that produce many seeds because dispersal can be rapid. Also the establishment of a long-lived seed bank makes total elimination difficult and continued vigilance over many years imperative. Usually the opportunity

for eradication is lost by the time the problem is recognized and the project considered or finally put into place. A vivid example of a lost opportunity was the failure to eradicate the tropical marine alga *Caulerpa taxifolia* (Vahl) (Chlorophyta, Chlorophyceae) from Monaco where it was first recognized in 1984 (Meinesz 1999). Eradication was called for in 1991 but to no avail. This "aquarium" plant is now widespread in the Mediterranean where it forms dense stands.

Successful eradications of small populations of recently introduced non-indigenous species may not be recorded in the literature and therefore it is difficult to judge how often this is successful. One such success in southeastern Queensland was the eradication of *Eupatorium serotinum* Michx. (Asterales, Asteraceae) in the 1950's (R. McFadyen pers. comm.). An on-going project in Australia is the attempt to eradicate Siam weed, *Chromolaena odorata* (L.) R.M. King and H. Robinson (Asterales, Asteraceae). Although densities have been greatly reduced, and the distribution has been limited to a 50 km radius, total eradication will be a slow process (R. McFadyen, personal communication).

In a recent review (Myers *et al.* 2000) 6 factors were proposed as necessary for a successful eradication program:

- 1) Sufficient resources to complete the project;
- 2) Clear lines of authority for decision making;
- 3) A target organism for which the biological characteristics are compatible with eradication (easy to find and kill, no seed bank);
- 4) Easy and effective means to prevent reinvasion;
- 5) Easy detection of plants at low densities; and,
- 6) Plans for restoration management if the species has become dominant in the community; there is little value in replacing one weed with another.

For widely established weeds, area-wide management may still be possible. This will involve continuous efforts to suppress populations of the plants chemically and mechanically in all locations. Working along the borders of the plant distribution may help to reduce the spread of the invasive weed, but metastatic spread of an invasive species following seed dispersal by animals or movement of plants by human activities works against successful containment.

In conclusion, rapid action following the identification of a newly established species may allow successful eradication, but procrastination can cause the window of opportunity to slam shut.

PRIORITY THREE - BIOLOGICAL CONTROL

For well established non-indigenous species biological, chemical, or mechanical control are the only mechanisms to reduce plant vigor and density. In most instances, chemical and mechanical control are too expensive and damaging to other members of the plant community and to the environment for widespread use. Although biological control usually is better focused on the target weed species than are the other control procedures, it does require the introduction of another species. In addition, in several cases biological control agents have moved onto non-target species of native plants (Louda *et al.* 1997, Louda 1999, Pemberton 1995). Therefore, careful consideration must be given to which species of biological control agents are introduced. Each introduction of an insect or plant disease will carry with it some chance that an unwanted non-target impact will result (Cory and Myers 2000, Follett and Duan 1999).

Selecting those species of natural enemies with the greatest potential for success is a challenge to the biological control practitioner.

Biological control, if successful, will reduce the density of the plant to a level at which other control is not required (McFadyen 2000), but it will not eliminate the weed species totally. However, biological control is not always successful. Estimates of how successful biological control is have varied from 10 to 30% of the weed species for which it has been attempted (Crawley 1989, McFadyen 1998, Myers, *et al.* 1988) to 80% success in Australia and South Africa (McFadyen 2000). Some of this variation may be influenced by how success is evaluated. And how much effort has been put into programs. If successful control requires a whole complex of natural enemies to reduce the density of the host plant populations, achieving success may be slower and more difficult than if single agents are able to reduce the densities of the target weeds.

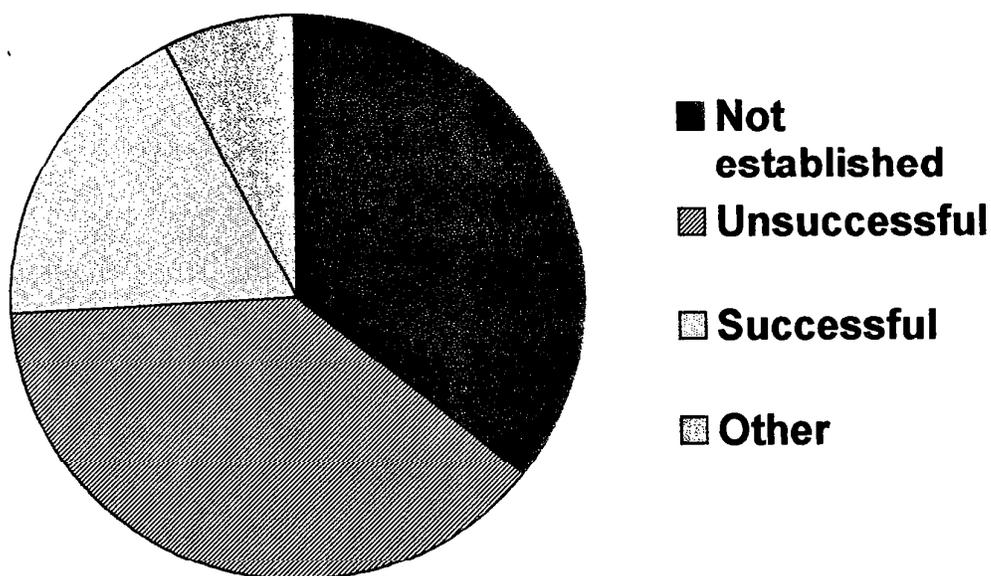
In an attempt to evaluate the question of whether a complex of agents is necessary for successful biological control, several studies have examined successful biological control programs recorded in the literature to determine whether success was attributed to several agent species or to just one. In the first of these studies (Myers 1984), 81% of successful biological control programs were attributed to one species of agent. In a more recent review (McFayden 2000) 41% of 41 successful biological control programs of weeds involved only one agent or success was attributed to one agent. Another study, based on data from Julien and Griffiths (1998), found that 54% of programs involving the introduction of several agents attributed success to a single agent (Denoth *et al.* in press). These studies are difficult to interpret because most often careful evaluation of the impacts of the various agents is not done. Therefore, attributing success to a particular agent or group of agents may be a bit arbitrary. There may be a tendency for biological control practitioners to attribute some success to every agent that has been introduced. This may explain why of 8 biological control successes recorded for Hawai'i (*Opuntia cordobensis*, Spegazzini (Caryophyllales, Cactaceae), *O. ficus-indica* (L.) Miller, *Ageratina riparia* (Regel) R.M. King & H. Robinson (Asterales, Asteraceae), *Emex spinosa* (L.) Campd. (Polygonales, Polygonaceae), *Rubus argutus* Link (Rosales, Rosaceae), *Tribulus cistoides* L. (Zygophyllales, Zygophyllaceae) (native) and *T. terrestris* L.) only 2 weeds (25%) are thought to have been controlled by a single agent and the other 6 successes, including the control of a native species, are attributed to a combination of agents (information from (Julien and Griffiths 1998)). This contrasts to 8 successful weed control programs in South Africa for which success in 5 programs (62%) is attributed to a single agent (Olckers and Hill 1999).

Historically on average 5 to 7 agents have been introduced for each biological control program although some weed species such as lantana have been the target for over 20 species of natural enemies (Broughton 2000). Of the thousands of biological control agents introduced globally, only about 10% have had sufficient impact on the host plants to be considered effective. The record of outcomes of agents introduced for biological control of weeds in Hawai'i is shown in Figure 1 based on data reviewed by Julien and Griffiths (1998).

This review of introductions and successes in biological control indicates that a number of non-indigenous agents are being introduced to control other non-indigenous species. Because the introduction of each species is associated with the possibility that it will have non-target impacts, it is important to be parsimonious in choosing agents for introduction. If certain types of potential biological control agents have had a poor record of success in the past, they should probably not be considered for introduction in future programs. We propose that one group of natural enemies that

are unlikely to have much impact on host plant density are those that merely reduce seed production.

Figure 1. Fate of the 81 species of agents introduced to Hawai'i for the biological control of weeds.



Seed predators are unlikely to be successful biological control agents because seedling survival is frequently related to the density of the seeds; high densities survive less well than low densities. This principle of "self-thinning" is well known in plant ecology (Silvertown and Lovette Doust 1993). The ability of plants to compensate for reduced seed production and lower seedling numbers makes the impacts of biological control programs difficult to predict (Myers *et al.* 1988). Most serious weeds have high seed production and therefore are likely to be able to absorb high seedling mortality from effective and/or numerous seed predators. Therefore, it would seem that seed predators have little potential as biological control agents for plants that are able to compensate for the loss of seeds and for those for which seedling establishment is limited by the number of "safe sites" available (Andersen 1989).

Although seed predators may not reduce the density of invasive weeds it is a widely held view that they may slow the spread of the target plants. In South Africa biological control practitioners consider seed predators to be useful in programs that use both chemical and mechanical control in addition to biological control (Impson *et al.* 1999). However the contribution of seed predators in these programs has not been evaluated. If the spread of plants is by diffusion, reduced seed production is more likely to be translated into a reduced rate of spread than if plants disperse as a metastatic process, with new establishments occurring outside the initial introduction

site and serving as new foci for spread of the species (Clark *et al.* 1998, Kot *et al.* 1996, Moody and Mack 1988). It cannot be assumed that seed predators will have a measurable impact on the rate of spread of plants. However, experimental analysis of this could be very useful for target weed species.

One way to evaluate the effectiveness of seed predators as biological control agents is to determine if they ever have been successful. Tephritid flies are seed predators, and they have been introduced in 25 biological of weed programs (Julien and Griffiths 1998). They never have been shown to be successful control agents. A review of South African weed control programs lists seed predators as only being successful when in combination with other agents (Olckers and Hill 1999). In these programs stem borers were the most successful agents followed by sap-suckers.

Rees and Paynter (1997) developed a model of scotch broom, *Cystisus scoparius* (L.) Link (Fabales, Fabaceae), from which they concluded that a reduction in plant fecundity could reduce broom density when the disturbance rate is high, and plant fecundity and seedling survival low. However, these situations do not hold for most introduced populations of broom and Paynter *et al.* (1996) concluded that seed predators were unlikely to reduce broom populations in New Zealand. They did suggest that seed predators might slow the spread of the species, but this is contradicted by observations in Oregon where the introduced insect *Exapion fuscirostre* (F.) (Coleoptera, Curculionidae) reduced seed production by 85% but did not reduce either broom density or spread (Andres and Coombs 1992). A recent matrix model of scotch broom showed that in prairie in Washington State, USA 99.9% of the seed would have to be destroyed to suppress invasion of the plant, but in urban sites with poor soil and disturbance only 70% of the seeds would have to be reduced to slow invasion (Parker 2000). These studies suggest that seed predators are not likely to be effective biological control agents for broom.

Several studies of native plants have indicated a relationship between seed predators and plant recruitment and density (Louda 1982a, 1982b, 1983, 1999, Louda and Potvin 1995). This difference in the impact of seed predators on populations of introduced and native plants may be related to the role of competing plant species in the native plant communities. Serious weeds often occur at such high densities that intraspecific competition is more important than interspecific competition. The potential relevance of competition to the impact of seed predators is seen in the one example that we know of in which biological control success has been attributed to a seed feeder. This is the control of nodding thistle, *Carduus nutans* L. (Asterales, Asteraceae), in North America by the weevil *Rhinocylus conicus* Froelich (Coleoptera, Curculionidae) (Harris 1984, Kok and Surles 1975), a biological control agent that has also been shown to have an impact on rare, native thistles (Louda 1999, Louda and Potvin 1995).

Nodding thistle is an annual plant and depends on disturbance for establishment, but once established it can dominate a site, at least temporarily (Wardle *et al.* 1995). A comparison of nodding thistle biology to another weed, diffuse knapweed, *Centaurea diffusa* Lam. and Frauenfeld (Asterales, Asteraceae), may indicate why a seed feeder is successful for nodding thistle but not for more typical weeds that are longer lived and better competitors. Knapweed is a short-lived (2-5 years) perennial and is able to invade sites that have experienced little disturbance (Berube and Myers 1982). Knapweed has very high summer survival of the rosette stage (90 -95%) while rosette survival of nodding thistle can be low (10-30%) (Sheppard *et al.* 1994). A simulation model of knapweed population growth indicated that because seedling survival was

density dependent, the only way to reduce weed density would be via an agent that killed rosettes (Myers and Risley 2000). Similarly, Kelly and McCallum (1995) found that density-dependent survival from seedling to flowering in nodding thistle plants compensated for seed loss, the higher mortality among rosettes in nodding thistle may mean that reduced seed production is sometimes translated into reduced plant density. Although seed predators may be effective in reducing the density of annual plants that are poor competitors, most invasive weeds are longer-lived and good competitors.

Seed predators may be attractive as biological control agents because they are relatively easy to find, particularly if they develop in the seed heads. Also, biological control success is often measured simply by the number of plants attacked rather than impacts on plant density (McFadyen 2000). This also makes seed predators attractive as candidates for biological control programs because they can be readily evaluated. The over-use of seed predators is demonstrated in the biological control program targeted against the yellow star thistle, *Centaurea solstitialis* L. Six species of seed predators have been introduced to North America against this weed (Pitcairn *et al.* 1999). Although at some sites seed and seedling density have been reduced for several years, no reduction of plant density has been reported for this annual plant. Would one species of seed predator have been as effective as 6?

Predicting the type of an agent that will be successful in reducing the density of a target weed is difficult. Study of the biology of the target plant may give some clues to "weak" points in the life cycle. If a plant produces lots of seeds it is unlikely that reduction in seed production will be translated to a reduction of plant density. Experiments in which the ability of plants to compensate for various types of damage may give clues of the type of agents that are likely to be effective. In addition, Force (1972) and Zwölfer (1973) have proposed that the most effective biological control agents are likely to be those that are not very common in the native distribution of the plant. If a species of natural enemy occurs at low density in the native habitat because it is a poor competitor or has a high level of parasitism it may demonstrate a good reproductive response when introduced to a new habitat, free of competitors and parasitoids. Therefore, being rare in the native habitat and having a high reproductive rate when reared in the absence of natural enemies or competitors may be characteristics to look for in potential biological control agents.

Because the introduction of non-indigenous species dilutes the native biodiversity of an area, the introduction of new species should be undertaken in a conservative manner. Just because a species has passed the host specificity tests does not necessarily mean it should be introduced. The possibility of non-target impacts should always be a concern. Therefore, efficacy should be another consideration in choosing potential biological control agents. A study of the biology of the target weed, including its ability to compensate for the loss of various life stages, should be a prerequisite for biological control introductions. A good example of compensation for herbivory is shown by lantana, *Lantana camara* L. (Lamiales, Verbenaceae), which survived experimental defoliation for 2 years (Broughton 2000). Defoliators are unlikely candidates to successfully control this plant species. Prediction of the impact of natural enemies on host plant density is certainly not easy. One way to evaluate control agents may be to create high-density patches in the native habitat and determine which species of natural enemies move onto the plants. By evaluating the impacts of potential agents in the native habitat, informed decisions can be made prior to introduction in the new habitat. Better evaluation of on going biological control programs could also provide information to allow improved understanding of what

things work and why. From current information, seed predators do not appear to be effective agents. Therefore their further introduction in biological control programs is unlikely to be a parsimonious approach to biological weed control.

CONCLUSION

By far the best approach to limiting potentially invasive weeds is limiting the introduction of plants to new areas. Better communication of the consequences and environmental costs of non-indigenous species may help balance the pressure applied on regulatory agencies by industries involved in commercial plant importations. Eradication attempts must be bold and fast. But because eradication is so difficult to achieve, proponents of the program should not make unrealistic promises. Finally, biological control does have potential for controlling the impact of foreign weeds. However, finding agents that are capable of reducing the densities of plants is not an easy task. Successful biological control is associated with agents that are capable of killing or greatly reducing the vigor of their host plants at a life stage for which little compensation can occur. A greater focus on the efficacy of proposed agents can help reduce the number of non-indigenous species that are introduced in biological control programs.

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LITERATURE CITED

- Andersen, A. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia* **81**: 310-315.
- Andres, L., and E. Coombs. 1992. Scotch Broom *Cytisus scoparius* (L.) Link (Leguminosae). pp. 303-305, In: *Biological Control in the U.S. Western Region: Accomplishments and Benefits of Regional Research Project W-84 (1964-1989)*. J. Nechols, L. Andres, J. Beardsley, R. Goeden and C. Jackson (Eds). Division of Agriculture and Natural Resources, University of California, Berkeley, CA.
- Berube, D., and J. Myers. 1982. Suppression of knapweed invasion by crested wheat grass in the dry interior of British Columbia. *Journal of Range Management* **35**: 459-61.
- Broughton, S. 2000. Review and evaluation of lantana biocontrol programs. *Biological Control* **17**: 272-286.
- Clark, J., C., Fastie, G. Hurtt, S. Jackson, C. Johnson, G. L. King, M., and J. Lynch. 1998. Reid's paradox of rapid plant migration. *BioScience* **48**: 13-24.

- Cory, J., and J. Myers. 2000. Direct and indirect ecological effects of biological control. *Trends Ecology and Evolution* **15**: 137-139.
- Crawley, M. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* **34**: 531-564.
- Denoth, M., L. Frid, and J. H. Myers. 2002. Multiple agents in biological control: Improving the odds? *Biological Control* (In Press).
- Follett, P.A. and J.J. Lynch. (eds.). 1999. *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, The Netherlands
- Force D.C. 1972. r- and K- strategists in endemic host-parasitoid communities. *Bulletin, Entomological Society of America* **18**: 135-137.
- Harris, P. 1984. *Carduus nutans* L., nodding thistle and *C. acanthoides* L., plumeless thistle (Compositae). pp. 115-126, In: *Biological Control Programs Against Insects and Weeds in Canada 1969-1980*. J. Kelleher and M. Hulme (Eds). Commonwealth Agricultural Bureau, Slough, U.K.
- Hazard, W. 1988. Introducing crop, pasture and ornamental species into Australia - the risk of introducing new weeds. *Australian Plant Introduction Review* **19**:19-26.
- Impson, F., V. Moran, and J. Hoffman. 1999. A review of the effectiveness of seed-feeding bruchid beetles in the biological control of mesquite, *Prosopis* species (Fabaceae), in South Africa. pp. 81-88, In: *Biological Control of Weeds in South Africa (1990-1998)*. T. Olckers and M. Hill, (Eds). Entomological Society of Southern Africa, Johannesburg, SA.
- Julien, M., and M. Griffiths. 1998. *Biological control of weeds: a world catalogue of agents and their target weeds*. CAB International: Wallingford, Oxon.
- Kelly, D., and K. McCallum. 1995. Evaluating the impact of *Rhinocyllus conicus* on *Carduus nutans* in New Zealand. pp. 205-211, In: *VIII International Symposium on Biological Control of Weeds*. E. Delfosse and R. Scott. (Eds). DSIR/CSIRO, Melbourne, Australia, Canterbury, New Zealand.
- Kok, L., and W. Surles. 1975. Successful biological control of musk thistle by an introduced weevil, *Rhinocyllus conicus*. *Environmental Entomology* **4**:1025-1027.
- Kot, M., M. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* **77**: 2027-2042.
- Landolt, E. 1993. Über Pflanzenarten, die sich in den letzten 150 Jahren in der Stadt Zürich stark ausgebreitet haben. *Phytocoenologia* **23**: 651-663.
- Louda, S. 1982a. Limitation of the recruitment of the shrub *Haplopappus squarrosus*

- (Asteraceae) by flower- and seed-feeding insects. *Journal of Ecology* **70**: 43-53.
- Louda, S. 1982b. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs* **52**: 25-41.
- Louda, S. 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae) along a climatic gradient. *Ecology* **64**: 511-521.
- Louda, S. 1998. Population growth of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on two species of native thistles in prairie. *Environmental Entomology* **27**: 834-841.
- Louda, S. M. 1999. Negative ecological effects of the musk thistle biocontrol agent, *Rhinocyllus conicus* Foel. pp. 215-243, In: *Nontarget Effects of Biological Control*. P. A. Follett and J. J. Duan, (Eds). Kluwer Academic Publishers, The Netherlands.
- Louda, S., and Potvin, M. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* **76**: 229-245.
- Louda, S., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. *Science* **277**: 1088-1090.
- Mack, R., D. Simberloff, W. Lonsdale, H. Evans, M. Clout, and F. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**: 689-710.
- McFadyen, R. E. 1998. Biological control of weeds. *Annual Review of Entomology* **43**: 369-393.
- McFadyen, R.E. 2000. Successes in biological control of weeds. pp. 3-14, In: *Proceedings X International Symposium Biological Control of Weeds*. N. Spencer, (Ed). Montana State University, Bozeman, MO.
- Meinesz, A. 1999. *Killer Algae*. University of Chicago Press, Chicago.
- Moody, M., and R. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**: 1009-1021.
- Myers, J. 1984. How many insect species are necessary for successful biocontrol of weeds? pp. 77-82, In: *Proceedings VI. International Symposium on Biological Control of Weeds*. E. Delfosse, (Eds). Agriculture Canada, Ottawa.
- Myers, J., and C. Risley. 2000. Why reduced seed production is not necessarily translated into successful biological weed control. pp. 569-581, In: *Proceedings X International Symposium Biological Control of Weeds*. N. Spencer, (ed). Montana State University, Bozeman, MO.

- Myers, J., C. Risley, and R. Eng. 1988. The ability of plants to compensate for insect attack: Why biological control of weeds with insects is so difficult. pp. 67-73, In: *VII. International Symposium on Biological Control of Weeds*. E. Delfosse (Ed). Instituto Sperimentale per la Patologia Vegetale, Rome Italy.
- Myers, J., D. Simberloff, A. Kuris, and J. Carey. 2000. Eradication Revisited: dealing with exotics. *Trends in Ecology and Evolution* 15: 316-320.
- Olckers, T., and M. Hill. 1999. *Biological Control of Weeds in South Africa (1990-1998)*. African Entomology Memoir No.1. Entomological Society of Southern Africa: Johannesburg, SA.
- Panetta, F. 1993. A system for assessing proposed plant introductions for weed potential. *Plant Protection Quarterly* 8:10-14.
- Parker, I.M. 2000. Invasion dynamics of *Cystisus scoparius*: a matrix model approach. *Ecological Applications* 10: 726-743.
- Pemberton, R. W. 1995. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in the United States: An immigrant biological control agent or an introduction of the nursery industry? *American Entomologist* 41: 230-232.
- Pheloung, P. 1995. Determining weed potential of new plant introductions to Australia. A report on the development of a weed risk assessment system commissioned and endorsed by the Australian Weeds Committee and the Plant Industries Committee. Agricultural Protection Board, Western Australia.
- Pitcairn, M., D. Woods, D. Joley, C. Turner and J. Balciunas. 2000. Population buildup and combined impact of introduced insects of yellow starthistle, *Centaurea solstitialis*, in California. pp. 747-751, In: *X Symposium, Biological Control of Weeds*. N. Spencer (ed). Bozeman, MO.
- Reichard, S., and F. Campbell. 1996. Invited but unwanted. *American Nurseryman* 187: 39-45.
- Reichard, S., and C. Hamilton. 1996. Predicting invasions of woody plants introduced into North America. *Conservation Biology* 11: 1993-203.
- Sheppard, A., J. Cullen, and J. Aeschlimann. 1994. Predispersal seed predation on *Carduus nutans* (Asteraceae) in southern Europe. *Acta Oecologica* 15: 529-541.
- Silverton, J., and J. Lovette-Doust. 1993. *Introduction to plant population biology*. Blackwell Scientific Publications, Oxford.
- Wardle, D., K. Nicholson, M. Ahmed, and A. Rahman. 1995. Influence of pasture forage species on seedling emergence, growth and development of *Carduus nutans*. *Journal of Applied Ecology* 32: 225-233.

White, P., and A. Schwarz. 1998. Where do we go from here: the challenges of risk assessment for invasive plants. *Weed Technology* 12: 744-751.

Zwölfer, H. 1973. Competition and coexistence in phytophagous insects attacking the heads of *Carduus nutans* L. pp. 74-80, In: *II International Symposium, Biological Control of Weeds*. P. H. Dunn (ed). Rome, Italy.