PLANT - INSECT INTERACTIONS AND THE BIOLOGICAL CONTROL OF WEEDS

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ABSTRACT - Many of the world's most serious weed problems arise following the introduction of plants into exotic habitats. The introduction of natural enemies, particularly insect herbivores, from the native range may control these weeds, and is likely to be the only solution. I propose that the most effective natural enemies will be those that are rare in the native habitat and in most cases a single species will be effective. Improving the ability to identify potentially successful agents through experimentation in the native habitat and using nitrogen fertilization to enhance plant quality and herbivore population density are suggested techniques to improve biological control. Heterogeneity of plant quality and clumped distribution of insects on plants may help in the persistance of agents when weed populations have been suppressed. Biological control is the only solution for many weed problems.

Index terms: biological control, weeds, plant-insect interactions.

INTERAÇÕES ENTRE PLANTAS E INSETOS NO CONTROLE BIOLÓGICO DE PLANTAS DANINHAS

RESUMO – Muitos dos problemas de plantas daninhas mais sérios no mundo originam-se após a introdução de espécies de plantas em ambientes exóticos. A introdução de inimigos naturais, particularmente insetos herbívoros, da região de distribuição natural da planta, poderá resultar em um bom nível de controle, e é provável que esta seja a única solução em muitos casos. Neste trabalho eu argumento que os inimigos naturais mais efetivos serão aqueles que são raros no ambiente nativo e que, freqüentemente, uma única espécie produzirá o efeito esperado. Implementando a habilidade de identificar agentes bem-sucedidos através da experimentação no habitat nativo, e usando fertilização nitrogenada para aumentar a qualidade da planta e a densidade da população de herbívoros, são técnicas sugeridas para melhorar a eficiência do controle biológico. A heterogeneidade da planta e a distribuição agregada dos insetos sobre a mesma pode contribuir para a persistência dos agentes de controle quando as populações de plantas daninhas forem suprimidas. O controle biológico é a única solução para muitos problemas de plantas invasoras.

Termos para indexação: controle biológico, ervas daninhas, interação entre plantas e insetos.

INTRODUCTION

The premise of biological weed control is that diseases and insect herbivores are capable of reducing host plant density. The low and a patchy distribution of many plants in native habitats as compared to their near monoculture density and distribution in exotic habitats may support this premise. However, other interactions such as competitors, climate, and soil conditions could also contribute to the striking differences often observed between plants in native and exotic habitats. These latter parameters are difficult or impossible to manipulate. But we can introduce natural enemies to new areas that have been invaded by exotic weeds, and in this way attempt to achieve at least some degree of reduction in plant density.

Biological control programs for weeds become experimental tests of the efficacy of natural enemies in determining the density of their host plants. We can ask a number of questions about plant-insect interactions based on the observed outcomes of biological con-

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trol programs: how successful are these programs? how many agents are necessary to achieve success? what type of agents are most successful? what components might be manipulated to achieve success? In the following I attempt to answer these questions based on our experience in biological control of weeds.

HOW SUCCESSFUL ARE BIOLOGICAL CONTROL OF WEEDS PROGRAMS?

Several studies have attempted to quantify the success of biological control programs. Ehler & Andres (1983) estimated that 29% of biological control of weed programs in the USA were successful (density reduced to an acceptably low economic level), and Myers (1985) estimated 30% success for projects worldwide. But Crawley and colleagues involved in the Silwood Project carried out a more extensive review of biological control programs and estimated that only in approximately 10-15% of cases was biological control successful following the introduction of native insect herbivores to exotic habitats (personal communication). Failures can arise from a variety of factors such as mismatching of hosts, impact of predators and parasites in the exotic habitat, poor condition of agents following transfer and accidental distruction of release sites (Myers 1987). However, in a number of cases establishment and population increase of the agents have occurred and visible damage to the weeds has resulted, but densities of weeds have not been reduced sufficiently to be considered under acceptable control (Crawley 1989).

HOW MANY SPECIES ARE NECESSARY FOR SUCCESS AND WHAT SORTS?

There are two schools of thought as to how biological control of weeds will be most successfully achieved. Harris (1981) holds the widely accepted view which I will call the "Enemy Complex View". Under this interpretation, to achieve successful control a large component of the total enemy complex must be established in the exotic habitat. With each additional species of herbivore the stress to the plants increases until a threshold is passed after which the density of the plant population declines (Harris 1981).

I hold another interpretation which I call the "Silver Bullet View" (Myers et al. 1989). This is based on the assumption that evolution will have lead to a situation in which common insect herbivores will be those that have little impact on the density of their host plants. On the other hand, species of insects that are rare in their native habitats because they themselves have numerous predators or parasites, or are poor competitors or are very susceptible to disease, will not have acted as a selective agent on their host plants. In addition these rare species will not have evolved any self-regulation mechanisms because they will not have experienced high densities. Therefore, when released into an exotic habitat with high host plant density these evolutionarily rare species will have a great impact on their host plants. They will attack plants in a way for which the plants will have little ability to compensate.

TESTS OF IDEAS

Testing whether the "enemy complex" or "silver bullet" situation most often explains successful biological control is difficult. The characteristics generally used to identify biological control agents are that they are at least sufficiently common to be found, that they are host specific, and that they can be reared in the lab for host testing. An additional characteristic that is often cited is that the species is common and widespread, the assumption being that this indicates adaptation to the broadest range of conditions. Given these characteristics it seems unlikely that most biological control programs will involve agents that normally occur at low densities. I have previously (Myers 1987) cited several examples in which there is some evidence for the interpretation that successful control agents were rare in their native habitat, but classification of insect density in the native habitat is not frequently reported in published accounts.

A possible addition to the list of successful control projects using agents that are rare in the native habitat is *Cyrtobagous salviniae*, the weevil that originated from southeastern Brazil and has successfully controlled ***Salvinia molesta*** in a number of areas including Australia and New Guinea (Room 1990 and refs. therein). *Cyrtobagous salviniae* occurred at all the sites surveyed in southeastern Brazil but only caused severe damage to salvinia in some of them. Each female weevil produces approximately 300 eggs, but these are laid over a period of about 200 days as compared to other insects that attack salvinia that reproduce more quickly (Forno 1981). Weevils disperse only when completely out of food plants and the species has no self regulating adaptations (Room 1990). After destroying monocultures of introduced salvinia the weevils maintain a low equilibrium on small plants in vegetation on the edges of the water body.

An example of a common herbivore failing to control a weed is seen in the program to control diffuse knapweed *(Centaurea diffusa)* and spotted knapweed *(C. maculosa)* in North America. In the native habitat 42 and 57 insect species have been reported to attack these plant species respectively, and 31% and 37% of these attack flowers or seeds. However, additional species that attack other plant parts such as the roots also primarily reduce seed production (Schroeder 1985). Insects that reduced seed production were concentrated on in the initial introductions because the knapweeds are prolific seed producers. In some North American sites seed production has now been reduced by over 95% by introduced biological control agents, but knapweed population densities have continued to be high. A relationship between seedling density and survival, and flowering plant density and seed production buffers the plant populations against seed predators. The reduction of seeds is compensated for by increased survival of seedlings. Plant removal experiments have shown that removal of 40-80% plants before the flowering stage can be completely compensated for in one growing season (Myers et al. 1990).

To conclude, evolutionary theory suggests that plants should adapt mechanisms to compensate for common herbivores or that herbivores should only be common if their impact on their food plants is not devastating. Only a minority of biological control programs are successfull and many of the unsuccessful programs have used the most common species of insect herbivores found in the native habitat. Several biological control successes have been achieved using agents that are rare in native habitats and a majority of successes have been achieved with a single species of biological control agent (Myers 1985). These observations support the "Silver Bullet" approach to biological control which is to find the rare species of insect herbivore that is capable of having a major impact on the host plant in the exotic environment.

MANIPULATING PLANT-INSECT INTERACTIONS FOR SUCCESSFUL CONTROL

Finding the silver bullet

Identifying possible biological control agents is almost always difficult. In the native habitat the weed species will most likely have a patchy distribution (Schroeder 1985). One way to determine which of the herbivores will best respond to being introduced into a high density of its host plants is to artificially increase the density of the host in the native habitat. This may be achieved by planting relatively large disturbed areas in the normal range of the host using seeds either collected in that area or from the exotic range where the plant is a pest. These plants may initially have to be protected through the use of insecticides or cages to achieve high densities. The impact of insects attracted to these sites could be studied and previously rare species that become common could be collected for host range testing and introduction.

Manipulating plant quality

Another characteristic of insect-plant interactions that has been exploited in some successful biological control programs is the relationship between plant quality, particularly that measured by nitrogen levels, and the survival and fecundity of the insect herbivores. Myers & Post (1981) found that fecundity and larval survival of cinnabar moth, *Tyria jacobae*, was related to the nitrogen levels of their host plants tansy ragwort, *Senecio jacobaea*. The relationship between plant nitrogen and insect success is generally assumed to an important aspect of plant-insect interactions (White 1984, Brodbeck & Strong 1987). Several cases of biological control success or agent establishment have followed the improvement of plant quality (Myers 1987).

The most recent example again involves the aquatic fern, salvinia, and the weevil, *C. salviniae*. Field cage experiments showed that weevils became more numerous on fertilized plants, and damage to the weeds could be increased through fertilization (Room et al. 1985). Once beetles are established, dead plant material breaks down at the edges of the beetle feeding areas and decaying plant material further fertilizes plants. This leads to a weevil outbreak and salvinia population decline.

We have observed in British Columbia that St. John'swort, *Hypericum perforatum*, plants in areas in which biological control was successful had higher nitrogen concentration than did plants in areas where control was not always successful. In addition, experimental fertilization of St. John'swort in the area with poor control lead to an increase in beetle larvae and adults and a striking decline of the plants in fertilized plots.

In conclusion, particularly in areas with low soil nitrogen, nitrogen fertilization could lead to increased herbivore loads and increased pressure from competing plant species, and reduced weed density.

PLANT QUALITY, INSECT DISTRIBUTION AND CONTINUATION OF SUCCESSFUL CONTROL

One of the first questions asked by the public in discussions of biological weed control is what will happen after control is successful? Will the insects begin eating valuable plants? The history of biological weed control is very encouraging in this regard (Harris 1990). Examples have been observed in which high densities of biological control agents will feed on other hosts after defoliating their primary host, but this condition has thus far been short lived and of little consequence (Harris 1990). No major problems have arisen from biological control agents switching their host preferences after introduction and the probability of this occurring is considered to be low (Lawton 1985).

A topic that has received considerable discussion of late is what characteristics maintain low plant density following successful biological control. Myers (1976) used simulation models to show that the clumping of insects on certain plants could stabilize populations. The successful control of *Opuntia inermis* by *Cactoblastis cactorum* has continued from approximately 1925 to the present in all but coastal areas of Queensland, Australia (White 1981). Even when cactus densities are low some moths can be found (Myers et al. 1981). Moths preferentially lay eggs on large, green plants in the vicinity of previously attacked plants. This heterogeneity of insect distribution will contribute to the persistance of the control agents and continued suppression of plant populations. While controversy about the relevance of pest-enemy models to predicting the outcome, stability, and persistance of biological control agents continues to rage (Murdoch 1990 and references therein), the most useful analysis will result from field observations (Myers et al (1981) and Room (1990) for examples). Successful control programs seem to persist and I know of no cases in which control has broken down over time.

CONCLUSIONS

Introduced weeds are going to continue to become problems as humans increase the rates of introduction through their own movements and activities. Biological controls are the only feasible solutions. Chemicals are too costly, temporary and threatening to the environment. On the other hand, monocultures of introduced weeds are threats to the persistance of native plants and the animals that feed on them as well as on the value of the land for recreation and economic use. The principles of biological control have been little changed since the early program against prickly pear cactus in Australia. Some projects work but many do not. More experimentation in the native habitat, changes in the characteristics used to select control agents, and attention to the evolutionary principles behind plant-insect interactions may help in improving the success rate of this crucial endeavor.

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