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An Experimental and Phytocentric Approach for Selecting Effective Biological Control Agents: Insects on Spotted and Diffuse Knapweed, *Centaurea maculosa* and *C. diffusa* (Compositae)

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Abstract

Because several control organisms have been studied in Europe and already established in North America, the biological control programme against spotted and diffuse knapweed, *Centaurea maculosa* and *C. diffusa* (Compositae) provides a good data set for evaluating methods of estimating effectiveness of biological control agents. The methods proposed by Harris (1973) and revised by Goeden (1983) yield similar scores of five root feeders compared with six seed feeders when ranked according to their criteria. However, they do not consider the effect of an agent on the weed's population ecology. The "ecoclimatic method" proposed by Wapshere (1970, 1985) could not be applied for the knapweed agents; main problems are listed and discussed. A new general protocol for selecting effective biological control agents is proposed, which emphasizes a more experimental and phytocentric approach and explicitly addresses effects on weed population ecology. When applied to these knapweeds it suggests that agents attacking the rosette stage are more effective in reducing knapweed density than seed-feeding agents. The four steps are discussed and illustrated using the knapweed project. The increased effort for assessing an agent's impact on resource allocation and population ecology of the target weed allows better prediction of effectiveness of biological agents and will, therefore, lead to a reduction in the number of species to be screened and introduced. This, in turn, lowers the risk of unwanted effects of introduced species.

Introduction

Reduction in weed density or biomass is the ultimate measure of biological control success. The effectiveness of biological control agent; i.e., their ability to reduce weed density, is therefore of critical importance. Host-specificity determination, however, remains the crucial factor in determining whether an agent should be introduced.

In their native range, weeds are generally attacked by a complex of herbivores exploiting different plant parts and belonging to different feeding guilds (Schroeder 1983, Wapshere 1985). Guidelines were eventually developed by biological control workers (Harris 1973, Goeden 1983, Wapshere 1985) to detect potentially effective control agents prior to studies on life history and host-specificity. They aim to save time, to reduce costs of screening organisms and essentially to make biological weed control projects run more efficiently.

Although the problem of choosing effective agents is a recurrent topic in the biological control literature (Wapshere 1970, 1985, Harris 1973, Winder and van Emden 1981, Sands and Harley 1981, Goeden 1983, Room 1985) little progress has been made in applying these protocols for the selection of effective agents. If an agent was safe (restricted host range) and showed some impact on general plant performance (mostly on its morphology) it was proposed for introduction, assuming that a successful establishment would provide enough evidence for its effectiveness (Harris 1973, Winder and van Emden 1981). I will discuss problems in applying these protocols for the knapweed programme as a model case, and suggest a more experimental approach.

The knapweed programme provides a good data set for evaluating methods for estimating effectiveness of biological control agents, since the biology of more than 15 agents has been studied in detail, of which seven are already established in North America and four species recommended for introduction (Müller and Schroeder 1989). During fields surveys carried out by the Commonwealth Institute of Biological Control (CIBC) (Delémont), and the USDA Biological Control of Weeds Laboratory (Rome), a total of 38 organisms (34 insect species), restricted to the genus *Centaurea* (Compositae) was found on spotted knapweed (*Centaurea maculosa* Lam.) and a total of 37 organisms (34 insect species) on diffuse knapweed (*C. diffusa* Lam.) (Schroeder 1985).

Here, I use effectiveness to describe an agent's ability to affect plant performance; i.e., its degree of "destructiveness". I will not discuss attributes related to its potential safety, ease of culture, or establishment.

This paper first summarizes attempts to control spotted and diffuse knapweed in North America. Second, methods previously applied to select effective biological control agents are discussed using the knapweed data. Third, experiments presently carried out to analyse the joint effect of two root feeders, plant competition and nutrient supply on resource allocation by spotted knapweed and consequences for its population ecology are described. Fourth, a more phytocentric and experimental protocol for selecting effective agents is proposed.

Insects infesting *Centaurea maculosa* and *C. diffusa* in Europe

Spotted and diffuse knapweed, a short lived perennial and a biennial, respectively, both of Eurasian origin, were accidentally introduced into North America in the early 1900s and have subsequently become important rangeland weeds in southwestern Canada and the northwestern United States (Harris and Myers 1984). The study of the phytophagous insect complex associated with these plants in Europe was initiated in 1961 by the CIBC, Delémont, Switzerland on behalf of the Canadian Department of Agriculture. Three flower head infesting insects, *Urophora affinis* Frauenfeld, *U. quadrifasciata* (Meigen) (Diptera: Tephritidae) and *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae) were first released in Canada between 1970, and the root miner *Sphenoptera jugoslavica* Obenb. (Coleoptera: Buprestidae) in 1976. All four biological control agents have become established. However, despite heavy seed predation and wide distribution of the flower head insects, no measurable decrease in weed density has so far occurred in Canada (Harris and Myers 1984, Myers, J.H., pers. comm. 1989).

A second faunistic survey started by the CIBC in 1977 aimed to investigate the insect species associated with the roots of spotted and diffuse knapweed in Europe in order to assess their suitability as potential biological control agents. As a result of these studies, the moths *Agapeta zoegana* L. (Lepidoptera: Cochylidae), *Pelochrista medullana* (Staudinger) (Lepidoptera: Tortricidae), *Pterolonche inspersa* Staudinger (Lepidoptera: Pterolonchidae) (studied by the USDA Laboratory, Rome) and the weevil *Cyphocleonus achates* Faber (Coleoptera: Curculionidae) were recommended for introduction. *A. zoegana*, *P. medullana*, *P. inspersa* and *C. achates* have been released in 1983, 1985, 1987 and 1987, respectively. *A. zoegana*, *P. medullana* and *P. inspersa* are now established in Canada, and *A. zoegana* in the USA (Müller and Schroeder 1989).

Before 1986, only very limited date were available on the population ecology of these knapweeds in their new habitat in North America. However, a recently developed population model (Myers, J.H., pers. comm., 1987) for diffuse knapweed suggest that the population dynamics is little affected by reduced seed numbers, but that rosette survival is essential in determining knapweed equilibrium density. Biological control agents that attack the rosette stage therefore suggested to be more effective reducing knapweed densities than the seed-feeding agents already established (Myers, J.H., pers. comm., 1987).

This view is supported by other studies on biennials and short lived perennials (Crawley 1983, and references therein). Room (1980) suggested that plants which invest more in seeds and dormancy and that form extensive seed banks in the soil are often subject to high density dependent seedling mortality (such as occurs with the short lived, monocarpic perennial knapweeds studied). Thus the most effective agents would be those that attack parent plants, rather than their seeds.

Application of Methods Commonly Used to Estimate Effectiveness of Potential Biological Control Agents for Knapweed Insects

The predictions described above on effectiveness of knapweed agents were compared with the rankings of previously used methods of estimating effectiveness.

The method developed by Harris (1973) provides a scoring system for the various attributes of an agent and its relation with the weed, using only data of an initial field survey. Goeden (1983) revised Harris scoring system by modifying some of the criteria but improved it mainly by ordering the agent's characteristics with regard to: (1) an agent's capacity to inflict damage to its host plant under field conditions ("destructiveness"); (2) its suitability as a biological control agent (ease of culture, potential safety); and (3) its potential effectiveness in the area of introduction (after detailed studies have been carried out).

Eleven insect species infesting the flower heads and roots of spotted and diffuse knapweed, seven of which are already introduced, have been rated according to these scoring systems (Fig. 1). Phase 1 of the revised system by Goeden (1983) deals only with an agent's ability to damage a target weed (based on field observations) and this score is also given separately since it corresponds with the term effectiveness used in this paper. The scores between the root- and flower-head-infesting insects or between organisms of different feeding types for each plant part are very similar for all three system used. An expected positive correlation was found between Harris' (1973) scores, but also between the scores using the criteria by Harris (1973) and Goeden's (1983) phase 1 only (destructiveness).

Wapshere (1985) scored five agents attacking the seedling to rosette stage of *Echium vulgare*, L.; Boraginaceae). All reached similar scores, although the agents differed in the plant part attacked, the feeding type and other characteristics. Hence, there appears to be no unambiguous choice between agents attacking different phenological stages of the weed or between agents attacking the same phenostage, but differing in their mode of feeding (Wapshere 1985). This simply reflects the fact that post-herbivore effects; i.e., the consequences of the agent's damage for the population ecology of the weed, have not been included in these scoring systems.

Wapshere (1985) emphasises the importance of measuring an agent's observed actual effect or estimated possible effect on its host plant in its native range. His proposed "ecoclimatic method" (Wapshere 1970, 1985) uses as the principal criterion the effect of an agent on the regulation of a weed population or biomass in certain ecoclimatic situations, with adjustments for any ecological and climatical differences between the native area and the area of introduction. Increasing priority is given to organisms that occur in equal or greater abundances in regions ecoclimatically similar to target areas than in other regions, to agents that are highly damaging to individual plants and, finally, to agents that are highly effective in reducing weed density. According to Wapshere (1985) problems using this method are: (1) matching sites at the appropriate stage in succession (same level of disturbance, similar plant density and vegetation texture; if this cannot be found in the native region, Wapshere (1985) suggest that the community should be disturbed in such a way that dense stands are created naturally; (2) the presence of several agents at the same site; (3) the level of parasitisation and predation; and (4) to account for climatic differences.

The problems in applying the "ecoclimatic method" for scoring the knapweed insects are summarized in Table 1. The main difficulty in using this approach is quantifying the role of the agents on plant population dynamics; i.e., relating changes in plant density to herbivory, and assessing the relevance of specific damage for survival or fecundity of the plant. In semi-natural habitats, C. *maculosa* occurs at a low density equilibrium where effective agents may have already done their job and are now reduced to low numbers. Here the weed density is probably regulated primarily by plant competition (Crawley 1983). In disturbed sites, *C. maculosa* reaches high densities but such sites have an extreme short duration time and population fluctuations are most likely the results abiotic factors and human activities (Schroeder 1985). The fact that the American target weed is a tetraploid, polycarpic, short lived perennial compared to the widely distributed diploid, monocarpic biennial, surveyed in Europe, presents a further complication. Experimental studies in root containers showed that the life cycle, biomass production, longevity as well as changes in rooting intensity due to root mining by *A. zoegana* differed considerably between the two plant demes studied (Müller 1987, 1989*a*).

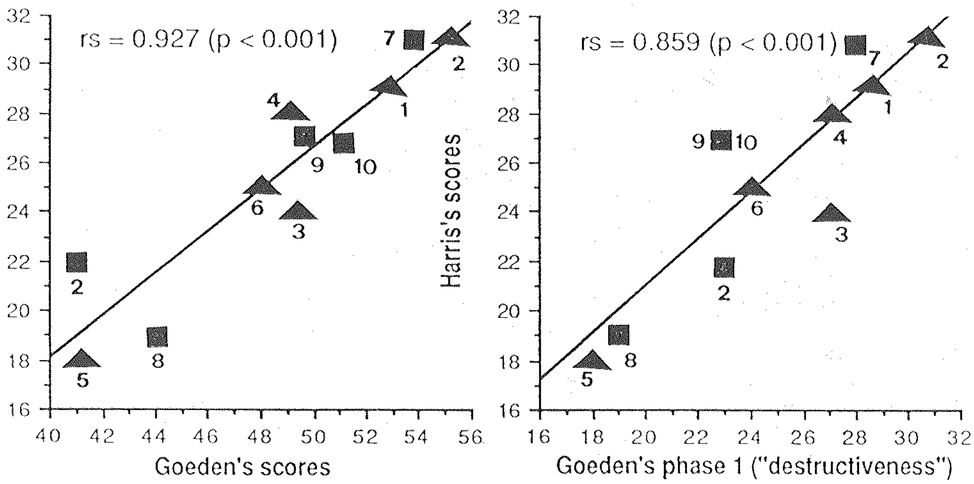

Figure 1. Comparative scores of insects attacking the roots and flower heads of spotted and diffuse knapweed, *Centaurea maculosa* Lam. and *C. diffusa* Lam., using Harris' (1973) and Goeden's (1985) (total and phase 1 only) criteria, and the correlation between these scoring systems (Spearman rank correlation coefficient, *N* = 111). Flower head insects (triangles): 1 - *Urophora affinis* Frauenfeld; 2 - *U. quadrifasciata* (Meigen); 3 - *Chaetorellia* sp. nov.; 4 - *Terellia virens*; 5 - *Metzneria paucipunctella* Zeller; 6 - *Larinus minutus*. Root insects (squares): 7 - *Agapeta zoegana* L.; 8 - *Pelochrista medullana* (Staudinger); 9 - *Pterolonche inspersa* Staudinger; 10 - *Cyphocleonus achates* Faber; 11 - *Sphenoptera jugoslavica* Obenb.. Data are from Gassmann *et al.* (1982), Marquardt, K. (pers. comm., 1988), Müller *et al.* (1982), Müller (unpubl. data), Stinson (1988) and Zwölfer 1976). Comparison of scores between insects attacking the flower heads and the roots (Mann-Whitney-*U*-test): Harris' scores: *U* = 13.5 (n.s.); Goeden's total scores: *U* = 14.5 (n.s.); Goeden's phase 1 only: *U* = 8 (n.s.).

In conclusion, none of these methods facilitated the decision to choose the first from *ca.* 10 potential agent species, that all showed an appropriate abundance and distribution for more detailed studies.

An Experimental Approach to Assess Effectiveness of Potential Biological Control Agents

Theoretical considerations

Successful biological control projects clearly demonstrate that phytophagous insects can reduce equilibrium plant populations well below their carrying capacities (Julien 1982). The effect of herbivores on the population dynamics of plants depends on the developmental stage of the plant attacked, the compensatory mechanisms involved and the transition probability of that stage (Crawley 1983, Mortimer 1984). Dirzo (1984) lists factors that determine the costs of herbivore damage for an individual plant. These factors are:

(1) the plant's phenostage. Removing a unit weight from a seed, seedling, rosette or adult plant may have completely different effects on plant performance; a plant becomes in general more tolerant to herbivore damage during its ontogeny (Dirzo 1984, Parker and Salzam 1985);

(2) the modular structure of a plant. How the plant is organized in terms of the items of consumption or sites for oviposition: the study of the influence of herbivory on the demography of plant modules may allow a better understanding of plant-herbivore interactions, such as mechanisms for plant compensation;

(3) the quality of damaged tissue. Different plant parts or given plant parts at different ages have different value for the plant (McKey 1979); and

(4) the quantity of the damaged tissue.

Table 1. Problems in estimating the effectiveness of biological control agents for spotted knapweed in the native range.

Observation in the native area	Problems
1. Plants in semi-natural habitats: low-level equilibrium (regulated by plant competition). Plants in ruderal habitats: dense populations, but unstable(regulated by biotic factors and human activities).	How to assess the role of herbivory on plant density?
2. Host plant: diploid, monocarpic, biennial. Target plant: tetraploid, polycarpic, short-lived perennial.	How to predict herbivore-induced reactions of the target weed?
3. High values for species packing: 2.9-6.5 root species and 2.5-4.0 flower head species/site.	How to quantify the effect of a single herbivore species on plant population dynamics?
4. High levels of parasitization; e.g., for the root-moth *Agapeta zoegana*; 1-60%; nine parasitoid species reared; incidence of attack and species composition of parasitoids varied greatly from site-to-site and year-to-year (Müller *et al.* 1989).	How to allow for effects of feeding parasitization and predation?

To measure the role of herbivory on plant density, consequences of herbivory on individual plants grown under controlled conditions have to be extended to the population and community level (post-herbivore effect). Additional interacting variables, such as the effect of neighbouring plants as well as the availability of water and nutrients for the plant have to be considered.

Experiments with insects infesting the roots of Centaurea maculosa

A. zoegana and *C. achates* overwinter as larvae in the tap roots of knapweed rosettes. The larvae of *A. zoegana* develop in the cortical tissue of the root (Müller *et al.* 1988). As small plants can be destroyed by a single larva, and larvae will search for additional plants if they deplete their food supply renders them highly effective in reducing rosette density. The larvae of *C. achates* develop in the central vascular tissue, where they form a gall-like enlargement of the tap root. The shoots of attacked plants are significantly shorter and produce fewer flowers than those of healthy plants (Stinson 1988).

The three major topics of a study presently being carried out are:

(1) how are growth, reproduction and dry matter distribution of C. maculosa *influenced by the following factors?* (a) root mining by *A. zoegana* and (b) by *C. achates*, which differ in their phenology of attack and feeding niche (transfer of larvae); (c) interspecific competition with the forage grass *Festuca pratensis* L. (Gramineae); and (d) different nutrient regimes (additional nitrogen supply);

(2) what statistical model best predicts the joint effects of these factors on plant performance (additive, multiplicative, other model); and

3) what are the long term effects of these factors on the life history and population dynamics of C. maculosa *growing at different densities?*

Two types of experiments have been set up to answer these questions. First, patterns of resource allocation are being determined in a factorial experiment (2 x 2 x 2 x 2 treatments), using potted plants in a greenhouse. We measure morphological parameters including growth rates and demography of plant parts. In addition plants will be chemically analysed for carbohydrates and nitrogen. Dry matter distribution and yield parameters will be determined after 14 and 18 months of growth. Secondly, changes in resource allocation due to four levels of root herbivory by *A. zoegana* (with 0, 1, 3, and 6 larvae per rosette), and due to intra- (25 and 100 plants/m^2) and interspecific (grass) competition, on the population dynamics of *C. maculosa* will be studied in field plots over a 3-yr period.

By using a full factorial design, it is possible to assess separate and joint effects of the various stress factors on estimates of root/shoot ratios, seed production, life stage distribution and plant densities. This study provides basic information on the reaction norm of plants infested with root herbivores in a range of environments. To investigate mechanisms leading to the observed pattern in resource allocation, nutritional and morphological characteristics of single plant parts can be determined.

Preliminary results of the field experiment showed a highly significant effect of knapweed density, grass competition and intermediate level of herbivory by *A. zoegana* on plant survival seven months after the start of the experiment and five months after transfer of larvae onto rosettes, respectively. Surprisingly, no significant interactions between these factors were found. Hence, an additive model adequately predicted the joint effects of herbivory, density, and grass competition. If low, intermediate, and high levels of herbivory were combined, no differences in plant survival compared to control plants occurred until five months after larval transfer. However, a significant negative linear relationship was found four months after larval transfer between herbivore level (log-scale) and rosette survival among the treatments with larvae present.

A New Protocol for Selecting Effective Biological Control Agents

> We can see that when a plant or animal is placed in a new country amongst new competitors, the conditions of life will generally be changed in an essential manner, although the climate may be exactly the same as its former home (Darwin 1859, cited by Mortimer 1984).

Whittaker (1979) stated, "that the main driving force determining plant distribution and abundance may be competition (with other plants), but the direction which this takes could be determined by the predator or herbivore". Even relatively low densities of herbivores can have a significant effect on the dynamics of plants if the dispersal rate and searching efficiency of the animal are high (Harper 1977) and if the plant is already stressed by other biotic or abiotic factors (Harris 1981). For example, the effect of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), on abundance of ragwort, *Senecio jacobaea* L. (Compositae), in Canada depends on the balance of environmental stresses that are acting upon the plant (Harris 1981). In British Columbia, *S. jacobaea* is defoliated in early summer, but is able to regenerate after feeding has ceased. Density fluctuations of the weed are therefore mainly related to climatic factors (Dempster and Lakhani 1979). The short growing season and slower regeneration of the weed on dry sites in Eastern Canada, however, delays its regrowth, the shoots become cold tender and the plants suffer winter mortality.

Table 2. Protocol for selecting effective biological control agents.

Step / Objectives	Study area and type of investigation
1. Study the weed's population ecology to determine transitions in the life cycle to which equilibrium density is most sensitive: **> targeted phenostage**	Field experiments in area of introduction (e.g., removal and clipping)
2. Detailed field study for organisms associated with the specific phenostage: **> list of phenostage-specific organisms.**	Field survey in native range.
3. Ranking of these organisms according to their effect on resource allocation; i.e., on growth, fecundity, and survival of the target weed grown under similar conditions as in the problem area (parallel screening of critical test plants): **> species priority list for exhaustive host-specificity screenings.**	Laboratory experiments with potted plants; field cage studies in the native range.
4. Separate releases of populations, species and species compositions and evaluation of their effect on resource utilization and weed density: **> selection of the most virulent populations in a given habitat for further spread and introduction.**	In area of introduction at ecoclimatically-similar sites.

The proposed four-step procedure of a biological control programme should therefore start with a study of the weed's population ecology, in particular the identification of transitions in the life cycle to which population growth is most sensitive (Mortimer 1984). Unfortunately, no published data exist on the population dynamics of spotted and diffuse knapweed. What we need to know first is how the density of knapweeds responds to varying levels of seedling establishment, rosette survival, seed production and perenniality of rosettes and flowering plants, which are all characteristics of knapweeds that may be modified by introduced biological control agents. Such data could be obtained by setting up experimental plots and removing varying numbers of seedlings, rosettes or seeds or by clipping plants or plant parts to simulate herbivory, and by monitoring the outcome for at least two years to determine seed production, plant recruitment and survivorship. Instead of making observations on the effect of the agent on the weed at the appropriate successional stage in the native habitat, as suggested by Wapshere (1985), experimental manipulation of plant densities where the weed should be controlled are far more realistic and easier to conduct. Advantages of doing such experiments in the area of introduction are obvious, as naturally-growing plants are abundant and climatic and ecological conditions such as density, level of disturbance and vegetation type (which are difficult or impossible to match in the native range) are the ones under which biological control agents will operate. Such experimental studies on the dynamics of the target weed population should produce a list of plant responses to various stress factors so that the phenostage which is most sensitive for density changes can be determined (Table 2). Sensitivity analysis provides a more formal and analytical approach for the study of plant demography (Caswell 1986).

In a second step, field surveys in the native area can be directed to look more carefully for organisms associated with a specific phenostage. For instance, if reduction of rosette density was found to have the most profound effect on equilibrium plant density, surveys should primarily be carried out when rosettes are available, and organisms infesting flower heads would get a lower priority. Herbivore species from closely related plant species (Hokkanen and Pimentel 1984) can be included to enlarge the species pool of potential agents.

In a third step, experiments of the type presented above for root feeders on *C. maculosa* have to be carried out to assess the effect of phenostage specific herbivores on plants experiencing comparable environmental conditions as the target weed in the area of introduction. Insects attacking different plant parts of the same phenostage (root- *vs.* rosette leaf-feeders) or organisms of different feeding type (gall-formers, miners, suckers, pathogens) could by ranked according to their effect on plant survival, growth, or fecundity (Winder and van Emden 1981, Harris 1985). Knowledge from field surveys with regard to feeding behaviour (territorial or colonial), species associations (possible interspecific competition), and plant phenostage preferences (small and bigger rosettes) (Stinson 1988, Müller 1989*b*) of control agents should be included and tested experimentally. In addition, different biotypes (Sands and Harley 1981) should be used to determine the most virulent strains. It is important that the invasive biotype of the weed be always used in such experiments, as has been illustrated for the case of spotted knapweed (Müller *et al.* 1988). Parallel studies on critical test plants should be carried out early to eliminate unsuitable species. The result will be a priority list for detailed host-specificity screenings.

In a last step, an effort should be made to release demes, if the number of individuals available permits it, of single species and species compositions separately at ecologically similar sites to be able to compare their suitability and effectiveness. These will depend in addition to the characteristics determined in steps 1 to 3, on their ease of establishment, their searching ability, intrinsic rate of increase and the potential loss by parasitism, predation and competition (Müller and Schroeder 1989). A careful analyses of these factors should aim to assess the "interaction norm" between control agents and the weed across different environments (Thompson 1986). The most effective species and most virulent strains can then be used for further spread and introduction at a given site.

Conclusions

The proposed protocol is not restricted to insect herbivores, but also applies to nematodes and plant pathogens. The main purpose of this paper is, however, to stress the need for experimental data on the population ecology of the weed, once it has been targeted for control, and before field studies in the native area are initiated. Protocols generally used for biological weed control underestimate the potential of such studies. Schroeder (1983) emphasises that studies carried out in the infested area should include a correct identification of the weed, data on the actual and potential distribution of the weed, its interaction with the native flora, ecological characteristics of the colonized area, the economic damage and beneficial value of the weed and an inventory of organisms present on the weed. With respect to predictions on the effects of control agents on the weed in the infested area, Wapshere (1985) states that "all than can be determined in the newly infested habitat is the rate of increase of the weed and its maximum density and biomass level".

Evidence from biological control programmes suggests that the chance of successful establishment and amount of control is generally not decreased by multi-species introductions (Cock 1986). It could therefore be argued that the time and money spent to determine the most effective agent is not rewarding and that all host-specific agents should be tried in turn to see which species or combination of species works best.

The limited knowledge on knapweed population ecology available today suggests, that with little investment in experiments to detect the phenostage most sensitive to population change, root-feeders should have been proposed as the prime candidates for biological control studies. The money spent for screening seed feeders would have been saved, although the higher effectiveness of the root-feeders remains to be seen. A careful analysis of the knapweed project will eventually permit this hypothesis to be tested and similar comparisons could be made for other biological weed control projects. The concern that introduced biological control agents may compromise the survival of endangered, native species has become more important in the last few years despite the excellent safety record of biological control (Harris 1985, Lawton 1985, Schroeder and Goeden 1986). The proposed protocol which emphasises the importance to determine the potential effectiveness of an agent prior to detailed host-specificity screenings will generally result in fewer species introductions and hence, lower the risk of unwanted effects by introduced control agents.

It is hopped that more plant demographers will be attracted to the fascinating experiments provided by biological control projects. This would greatly help to make predictions on the impact of biological control agents on weed populations more realistic and render biological control projects more efficient. It would also contribute to overcoming the barrier between ecology and pest control, which apparently still exists.

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