

The Ability of Plants to Compensate for Insect Attack: Why Biological Control of Weeds with Insects is So Difficult

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Abstract

Exotic weeds for which biological control is attempted are initially at very high density and intraspecific competition is the strongest biological process influencing plant density. Density related plant survival and seed production can buffer populations against even high levels of insect attack. Diffuse knapweed in British Columbia, Canada provides an example in which a 95% reduction in seed production has not been translated into a decline in the population density. Experimental removal of rosettes and flowering plants increases seedling survival and compensatory growth restores the density of knapweed in most cases over one summer. We predict that insects that are rare in their native environment will be most successful as biological control agents because plants will not have evolved compensatory responses to the type of damage they cause. Biological control studies will make a greater contribution to our understanding of plant - insect interactions if plant densities are quantified.

Introduction

Do insect herbivores reduce the density of their host plants? This question can be answered by experiments which compare plant density after the removal or the addition of insect herbivores. Introduction of insects for biological weed control is possibly the best experimental situation to evaluate the impact of insect herbivores because the researcher can manipulate insect species individually. The alternative, removing insects with insecticides, presents a variety of possible complications such as influences on other biotic processes and components of the system, which make interpretation more difficult. But these experiments are still valuable.

We can ask then how frequently or in what proportion of cases do introduced insects reduce the density of their host plants in biological control programs? This question is surprisingly difficult to answer. To evaluate it we can go to reviews that summarize information from a number of studies. Rather than quantified changes in the density of host plants after the introduction of the biological control agent, many evaluations are subjective; control was judged to be successful at least in some locations.

There may be a tendency for these results to be biased toward the positive side. For example, following the dramatic reduction of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in Australia by *Cactoblastis cactorum* (Bergroth) (Lepidoptera: Pyralidae), many other *Opuntia* have been the focus of biological control attempts and may have been controlled by either *Cactoblastis* or *Dactylopius* (Hemiptera: Dactylopiidae) (Moran and Zimmermann 1985). However, of 86 plant species reviewed by Julien (1982), 26 (30%) were considered successfully controlled (Myers 1985). Ehler and Andres (1983) report a success rate of 29% for weed projects in North America. This value will be estimated more accurately by the Silwood project, but Michael Crawley (personal communication, 1988) has suggested that only 10% of biological control projects have been successful. Since plant density is rarely measured, this evaluation tells us nothing about possible cases in which insects slightly reduced the density of their food plants.

In what situations are insects most likely to reduce the density of their host plants? To answer this we must measure the impact of insects on plants in different conditions. For example, *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) reduced the density of St. John's wort, *Hypericum perforatum* L. (Clusiaceae), in hot, dry areas of British Columbia, while *C. hyperici* (Forster) and *C. quadrigemina* only periodically reduce the density of St. John's wort in cooler and moister areas (Williams 1985). Rainfall, soil quality, sun exposure and plant competition can all influence the impact of insects on plant density. Insects may reduce host density in only a restricted portion of the plant species distribution.

We can also turn the question around and ask, "What proportion of herbivorous insects might be expected to significantly reduce the density of their host plants?". Zwölfer (1973) proposed a very stimulating idea when he suggested that the most successful biological control agents will be species that are maintained at low density by competition, predation or disease. Myers (1987) has reviewed several examples that support this view. I would like to extend this idea by suggesting that insects maintained at low density in their native habitat will have had little impact on the evolutionary environment of their food plants. The plants will not have evolved compensatory mechanisms in response to the type of damage caused by the rare herbivores. Therefore, rare species may prove to be the most successful biological control agents. Because common species are more likely to be introduced as biological control agents, this phenomenon (if true) could reduce the success rate of biological weed control programs.

The low success rate of biological weed control might also suggest that plants have evolved to compensate for the type of damage they most commonly receive. If so it is very interesting to consider how plants might compensate for insect damage.

When plant density is high, intraspecific competition is a major force on plant growth and survival. High density distinguishes most exotic weeds from native plants, and could strongly influence the impact of insects on plants in exotic environments. Plants that have evolved with high levels of a particular type of insect damage, such as seed predation, are likely to "overproduce" when insect damage is missing. Thus, intraspecific competition will reduce survival resulting in self-thinning, and in this way plant density will be well buffered against even high levels of insect damage. Self-thinning is most likely to occur in early life history stages and the potential for this may vary among plant species. This could strongly influence the susceptibility of plant species to biological control.

In this paper we report on short-term experiments that measure the effect of removing diffuse knapweed rosettes on plant density and survival of seedlings. This was done to investigate experimentally the ability of diffuse knapweed to compensate for the loss of rosettes as might occur if an insect that killed a rosettes was introduced as a biological control agent.

A Case Study with Diffuse Knapweed

Diffuse knapweed, *Centaurea diffusa* Lamarck (Asteraceae), was introduced to British Columbia, Canada in the early 1900's and now infests approximately 90,000 ha. In many areas the weeds exist in virtual monocultures. In 1970 and 1971 two seed head flies were introduced, *Urophora affinis* Frauenfeld (Diptera: Tephritidae) and *U. quadrifasciata* (Meigen) (Harris and Myers 1984) and these have reduced seed production by 95%. At one site, White Lake, the beetle, *Sphenoptera jugoslavica* Obenberger (Coleoptera: Buprestidae), was also introduced, and with the flies, have reduced seed production to approximately 4% of original values (Myers et al., unpublished data.). This major reduction in seed production has not been translated into measurable decline in knapweed density (Fig. 1).

Knapweed plants can be classified into three life stages: seedlings (small plants with < 6 leaves); rosettes (non-flowering plants with > 6 leaves); and flowering plants. Rosettes range in size from being very small, barely above the seedling size, to being approximately 10 cm in dia. The age of rosettes is variable and can range from one to at least 5 years. The growth and development of diffuse knapweed plants is very plastic which, while frustrating to the biologist, allows the plant to respond rapidly to environmental conditions. Seed germination occurs in the autumn or early spring and is associated with rain (Roze 1981). Although

observations of the survival of the rosette stage of diffuse knapweed did not show a relationship between rosette density and survival, (Myers et al., unpublished data) we investigated experimentally the ability of diffuse knapweed to compensate for the loss of rosettes as might occur if an insect that killed rosettes were introduced to knapweed infested areas of British Columbia. In addition, experiments were designed to investigate interactions between life stages of knapweed plants as indicated by survival of seedlings and development of seedlings to rosettes and flowering plants.

KNAPWEED DENSITY White Lake

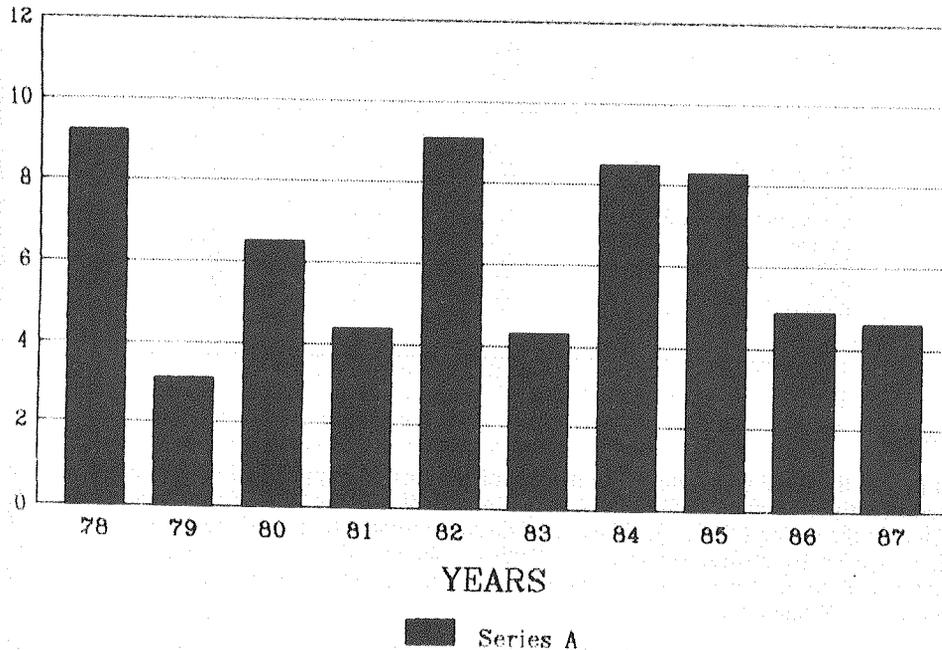


Figure 1. Density of flowering plants of diffuse knapweed measured in 0.25 m² plots each year along transects through the White Lake Study area. Number of quadrats varied from 10-50.

Materials and Methods

In May 1986, thirty square meter quadrats were marked out at each of three knapweed sites in British Columbia, Canada. Characteristics of these sites are outlined in Table 1. In each quadrat the number of rosettes and flowering plants were counted and 0, 40 or 80% of these two life stages were removed at ground level with a knife. Two or three people simultaneously and arbitrarily removed both bolting plants and rosettes until the proper percent was removed. The distribution of plants is likely to have remained similar even though the density was reduced. Surrounding soil was disturbed as little as possible. In a corner of the plot a 0.25 m² quadrat was marked and the number of seedlings counted. The quadrats were set out along linear transects at an interval of 10 paces with treatments alternating starting with a control plot followed by 40% removal, 80% removal and so forth.

In September 1986, the number of seedlings was counted in the corner 0.25 m² quadrats to determine how many survived, and the number of rosettes and flowering plants was counted in the total square meter quadrat.

In June and September 1985, all vegetation was clipped from another series of 0.25 m² plots to determine the biomass of knapweed and other plants at these same sites and one additional site (Table 1). In May 1986 plants of all three life stages were counted to determine the regeneration of knapweed following total removal in the previous summer.

Table 1. Characteristics of diffuse knapweed study sites in British Columbia. Density is number of flowering plants / 0.25 m² in June 1985. Precipitation is average totals of May and June from the nearest site monitored by Environment Canada. Forage was measured as grams / 0.25 m² dry weight of vegetation clipped in June 1985.

Parameter	Cache Creek	White Lake	Buse Hill	Grand Forks
Density	1.5(0.3)	8.3(1.2)	4.5(1.1)	7.3(1.0)
Precipitation (mm)	98	122	179	181
Elevation (m)	512	549	945	579
Forage	3.6	0.7	12.8	2.2
Cattle	N	N	Y	N
Flies	Y	Y	Y	Y
Beetles	N	Y	N	N

Results

In two of the three study areas, the density of rosettes on clipped and control plots was not significantly different 4 months following removal of 40% or 80% of rosette and flowering plants in the spring (Table 2). These two sites represent extremes of the rainfall gradient of sites invaded by diffuse knapweed in British Columbia (Table 1). The third site, where removal of rosettes was not compensated, has very dense knapweed and almost no other vegetation (White Lake, Table 1).

In all three sites, removal of 80% of the rosettes and flowering plants significantly improved the survival of established seedlings (Table 3). In two of the three areas removal of 40% of the rosettes and flowering plants also significantly improved seedling survival and the third area showed a similar trend ($P < 0.10$). It is clear from these results that larger knapweed plants reduce the survival of seedlings. Reduced density of older plants is compensated for by increased survival of younger vegetative stages.

Finally, we can determine the impact of total clipping of both knapweed and other vegetation on the density of the three life stages 3 or 12 months later. Total clipping reduced the density of flowering plants (Table 4). Spring clipping reduced significantly the density of rosettes at one site, while autumn clipping reduced significantly the density of rosettes at another site. Seedling numbers were only significantly reduced at one site by removal of all vegetation in the autumn. It is not surprising that clipping plants in the autumn reduces the density the next spring since plant growth and development is possible for only a short part of the intervening winter period.

Discussion

Biological control of weeds is experimental plant population ecology. By introducing insect herbivores we can measure the direct impact of herbivory on plant density. This contrasts to experimentally removing insects which is usually done by regularly applying insecticides (Brown *et al.* 1987, Cantlon 1969, Louda 1982, 1984, Waloff and Richards 1977). In both cases the impact of herbivores is usually evaluated with short term measures such as seed production or plant growth with and without herbivory. These measures may be inadequate for predicting changes in plant density if compensatory growth and survival occur. An exception is the study of Louda (1982) in which insecticide treatment showed the impact of insect herbivores on plant density in part of the range of the plant.

Table 2. Mean density of rosettes/m² in September 1986 for control plots and those in which 40 and 80% of rosette and flowering plants were removed in May 1986.

Area	Control	40% Removal	80% Removal
Cache Creek	13.5 (4.2)	8.7 (2.8)	9.9 (2.6)
Buse Hill	9.6 (1.7)	12.6 (3.2)	8.1 (1.0)
White Lake	25.0 (2.7)	17.0 (3.1) ¹	9.5 (2.1) ¹

¹ Density of rosettes significantly less on removal plants than on control plots ($P < 0.05$). Plots did not differ in density prior to treatment.

Table 3. Mean proportion seedlings surviving (s.e.) from May to September 1986 in 0.25 m² plots in which 0%, 40% or 80% of rosettes and flowering plants were removed in May 1986. Values are based on 10 quadrats for each treatment in each area.

Area	Control	40% Removal	80% Removal
Buse Hill	0.45 (0.12)	0.71 (0.12)	0.78 (0.12)
Cache Creek	0.44 (0.05)	0.61 (0.06) ¹	0.64 (0.10) ¹
White Lake	0.25 (0.08)	0.49 (0.06) ¹	0.80 (0.07) ²

¹ Survival of seedlings significantly better than on control plots.

² Survival significantly better than on control and 40% removal plots, t-test.

Weeds which are candidates for biological control differ from plants in their native habitat by being at very high density when insect herbivores are introduced. Therefore, we might not expect the impact of insects in this situation to be the same as that in native communities. In addition, if the plant density is reduced so that interspecific competition increases, herbivory might have a larger impact on plant density. The rapid growth and development of knapweed seedlings to rosettes following the reduction in the density of rosettes and flowering plants shows that for this system, intraspecific competition is a dominant biological interaction. Removal of larger plants increased the survival of seedlings and stimulated their development to the rosette stage. A very interesting result is the similarity of response of knapweed in sites in the driest part of their distribution where little other vegetation occurs and in an area

with more rainfall, Buse Hill, where other vegetation is more common (Table 1). Seedling establishment at this site is lowest of the five areas studied in 1986, which may be a result of interspecific competition (Myers, unpublished data), but intraspecific competition is obviously also strong.

Table 4. Mean density (SE) of knapweed in May 1986 for 0.25 m² plots clipped of all vegetation in June 1985 or September 1985 compared to similar unclipped areas. *N* = 10 for clipped quadrats and 30 for control quadrats.

Plant Stage	Control	Spring Clipping	Autumn Clipping
White Lake			
Seedlings	23.1 (2.3)	36.2 (7.9)	26.4 (5.02)
Rosettes	8.2 (1.1)	9.9 (2.3)	0.9 (0.4) ¹
Flowering	4.8 (0.6)	1.0 (0.5) ¹	0.1 (0.1) ¹
Grand Forks			
Seedlings	59.3 (6.4)	46.1 (9.6)	33.8 (8.2) ¹
Rosettes	6.9 (0.8)	2.2 (0.6) ¹	5.0 (2.7)
Flowering	6.3 (0.7)	1.7 (0.5) ¹	0.3 (0.2) ¹

¹ Values significantly less than controls with a t-test.

It is interesting to speculate on what proportion of weeds we might expect to be controlled by introduced insects and what proportion of insect herbivores we expect to have a measurable impact on the density of their host plants. Unless biological control programs are evaluated by quantification of plant density in areas with introduced herbivores and control areas, they will not help us gain information to turn our speculations into reasonable projections. The studies of diffuse knapweed show that at high density plants are able to compensate for large reductions in seed production, and density related growth and survival make populations resilient against this type of herbivore damage. An insect species capable of killing rosettes might have a greater impact on plant density, but it is not obvious that this type of insect exists.

We propose that plants may not be able to compensate for the type of damage done by rare insect species and therefore that these be given greater priority as candidates for introduction as biological control agents. One way of finding rare insects might be by planting areas of dense weeds in the native habitat to act as a collection site. And finally we propose that more work should be done to identify the relationships between density and survival and seed production of weeds that are potential candidates for biological control. By identifying the life stages most strongly influenced by intraspecific competition and evaluating possible interspecific interactions in the exotic situation we might be better able to predict and achieve biological control successes.

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