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## Why Reduced Seed Production is Not Necessarily Translated Into Successful Biological Weed Control

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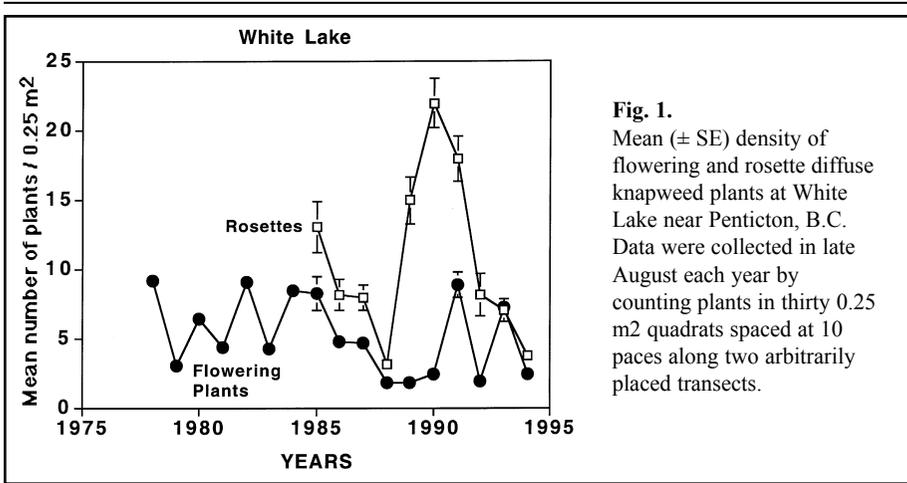
### Abstract

Insects introduced as biological control agents of diffuse knapweed, *Centaurea diffusa*, primarily reduce seed production. Knapweed densities appear to be resilient to greatly reduced seed production. We have used measurements of seedling density and survival, and production of seeds by flowering diffuse knapweed plants to develop functions for a model of knapweed populations. These simulations show that improved seedling survival can compensate for reduced seed production. The model indicates that the introduction of seed predators may even increase plant density under some relationships between seedling density and survival, and flowering plant density and seed production. We suggest that it is important to demonstrate that weeds are seed limited before introducing exotic herbivores whose impact is to reduce seed numbers. Successful biological control of knapweed may be achieved by insect herbivores that increase the mortality of later growth stages of plants such as the rosette stage for which survival is not as strongly related to density. Knapweed is likely to be typical of invasive weeds with high seed production and this study suggests that seed feeders are not likely to be successful control agents for most weeds.

**Keywords:** diffuse knapweed, biological control, *Urophora affinis*, *Urophora quadri-fasciata*, *Sphenoptera jugoslavica*, seedling survival, weed control, density-dependent survival, *Centaurea*

### Introduction

CLASSICAL BIOLOGICAL CONTROL of weeds involves the introduction of herbivores or fungi from the native habitat of the introduced plant to the exotic habitat where it has become a pest. Only approximately 15 to 20 % of weed biological control programs have been successful at reducing host density (Myers, *et al.* 1988). While failures are rarely studied, introduced biological control agents could be unsuccessful for various reasons. Introduced agents may never do well because poor climatic or plant biotype matching or the attack of predators and parasites in the new environment could prevent the agents from increasing in density. However, introduced agents may become established and reach high densities in the new environment, but still fail to reduce the density of the target weed. This was the case of cinnabar moth, *Tyria jacobaea* L. on tansy ragwort, *Senecio jacobaeae* L. Moth larvae can heavily defoliate stands of plants without causing a long term reduction in plant density (Myers 1980). It is possible that the low proportion of successful biological control programs is because, in general, insect herbivores or plant fungi have little impact on the density of their hosts, and therefore little potential as con-



**Fig. 1.** Mean ( $\pm$  SE) density of flowering and rosette diffuse knapweed plants at White Lake near Pentiction, B.C. Data were collected in late August each year by counting plants in thirty 0.25 m<sup>2</sup> quadrats spaced at 10 paces along two arbitrarily placed transects.

tol agents (Crawley 1989). This idea has not been explored, but most agents introduced for biological control of weeds are not successful (Myers 1984).

We consider here interactions between diffuse knapweed, *Centaurea diffusa* Lam. and biological control agents of Eurasian origin; two tephritid gall flies, *Urophora affinis* Frauenfeld and *U. quadrifasciata* Meigen, (Harris and Myers 1984, Myers 1987) and a root boring buprestid beetle, *Sphenoptera jugoslavica* Obenb. (Powell and Myers 1988, Zwölfer 1976).

The impact of all of these agents is primarily to reduce the production of seeds of knapweeds (Harris and Myers 1984). At one site to which *Urophora* and *Sphenoptera* were introduced in the mid-1970's knapweed has been as dense in some recent years as it was near the time of initial release of biological control agents (Fig. 1). We report here a simulation model to explore why the density of knapweed is so resilient to insects that reduce seed production.

## Methods

**Measuring plant density and survival.** In June 1985 and May 1986 quadrats (0.25 m<sup>2</sup>) were placed haphazardly in 5 study areas (Tab. 1) by walking along arbitrary transects with eyes closed and dropping a wooden frame at 10 pace intervals. The corners of the quadrats were marked with stakes for later identification. The number of seedlings (six or fewer complete leaves), rosettes, and erect flowering plants were counted in each quadrat. To determine survival of plants over the summer the quadrats were recounted in September of each year. At that time all of the flowering plants in the quadrats were removed and taken to the lab for counts of seed heads, seeds, and fly galls. At one site, White Lake, attack of plants by root boring beetles was noted by cutting the roots longitudinally and looking for larvae or evidence of damage from larvae. In 1985, 5-13 quadrat samples were collected from each site. In 1986, 20 (Ned's Creek) or 30 quadrats were counted (Tab. 1). Different quadrat locations were used in the two years.

## Knapweed Model.

The model was written in GW-BASIC and consists of functions linking the plant

Table 1.

Characteristics of areas from which plant data were collected and number of quadrats counted. All sites except Buse Hill are in the Ponderosa pine - bunch grass biogeoclimatic zone and Buse Hill is in the Interior Douglas-fir zone. Flowering plant densities are per 0.25 m<sup>2</sup>. Flies were introduced to all sites in mid- to late 1970's and *Sphenoptera* beetles were introduced to White Lake 1976. <sup>a</sup>Mean number of *Urophora* galls per 0.25 m<sup>2</sup>.

Site	Elev.	Summer Rainfall	Cattle	No. Quads		Mean density		<i>Urophora</i> <sup>a</sup>	
				1985	1986	1985	1986	1985	1986
Cache Creek	512 m	98 mm	n	13	30	1.5	1.5	20	3
Buse Hill	945 m	179 mm	y	10	30	4.5	3.6	175	61
Ned's Creek	427 m	119 mm	y	5	20	4.4	2.2	151	350
White Lake	549 m	122 mm	n	10	30	8.3	4.8	178	720
Grand Forks	579 m	181 mm	n	10	30	7.3	6.3	127	249

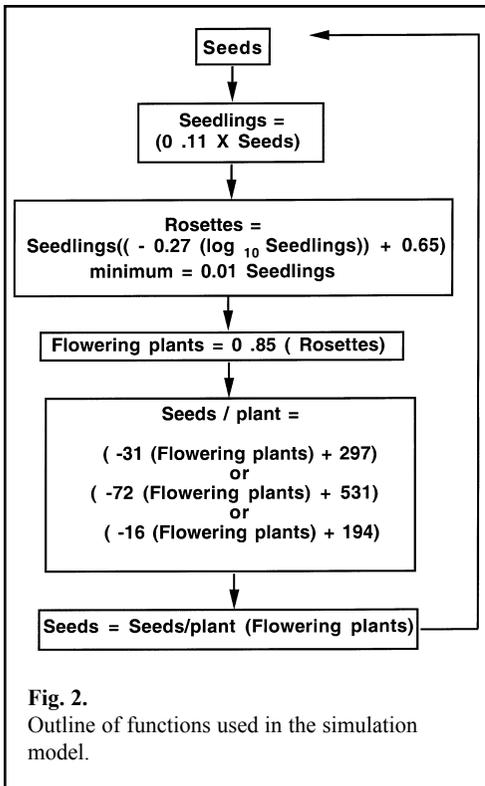
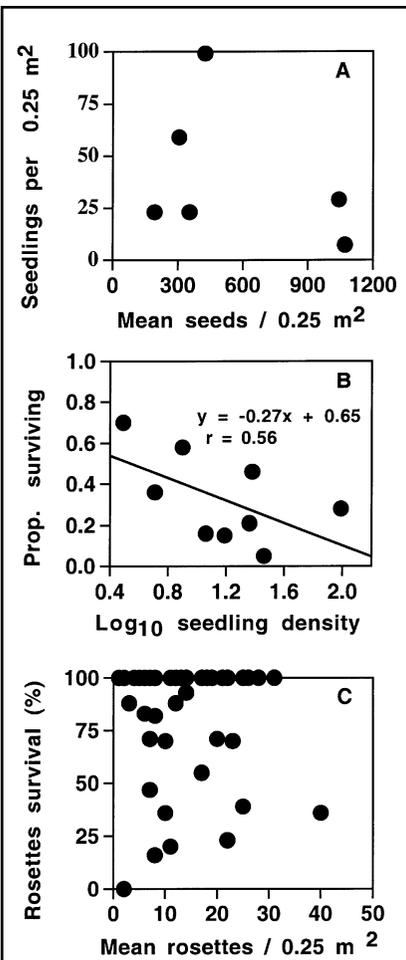


Fig. 2. Outline of functions used in the simulation model.

stages of diffuse knapweed from seeds produced, seedling establishment, seedling survival and rosette survival to flowering plant density and seed production (Fig. 2). These functions are described below.

1. Seedling establishment.

The transition between seeds produced one year (1984 (one site) or 1985 (five sites)) and seedlings the next (1985 or 1986) was estimated from the mean density of bolted plants and counts of seeds produced by plants harvested from quadrats in September. Seedling survival was estimated from the ratio of spring seedlings to seeds produced the previous autumn, and varied from .007 to .232. These levels of survival agree with other reports for seedling establishment of diffuse knapweed (Morrison 1987, Myers and Berube 1983, Roze 1981). We used an intermediate level of 11% survival for the



**Fig. 3.** A. The relationship between the mean number of seeds produced in the autumn for the 5 sites and the mean number of seedlings counted in the spring. Data were collected for the White Lake site from both autumn 1984 to spring 1985, and from autumn 1985 to spring 1986. B. Relationship between log<sub>10</sub> spring density of seedlings and proportion seedlings surviving. (See text for methods). C. Relationship between mean number of rosettes per 0.25 m<sup>2</sup> and percent survival of diffuse knapweed seedlings. (See text for methods).

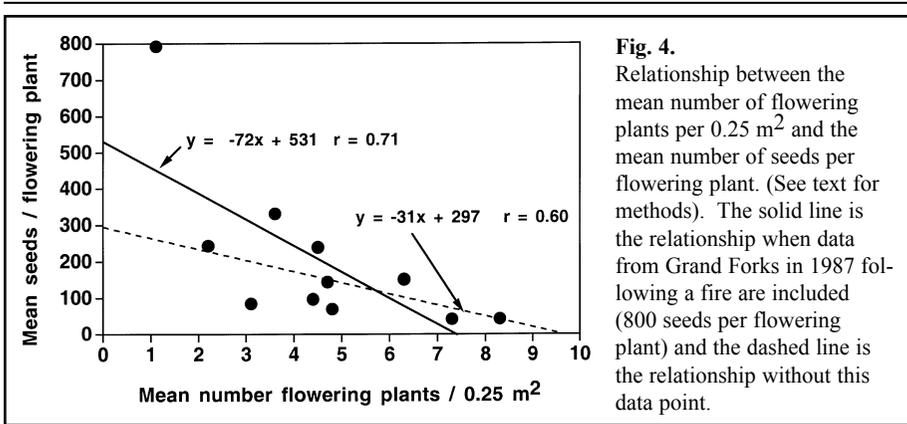
model. The transition of seeds to seedlings is influenced by two factors that were not distinguished for this study. Some seeds will germinate in the autumn and die in the winter so will not be seen as seedlings the next spring. This will be a loss of seeds. On the other hand, if seeds from the seedbank germinate this will be an addition to the spring seedling count. The contributions of these two factors might differ from year to year. Seedling numbers were not correlated to seeds produced for the 5 sites (Fig. 3 A) ( $r=0.04$ ,  $df=5$ ), and therefore only one estimated value was used for seedling establishment. Mean values were used because different quadrats were measured in autumn and spring.

## 2. Seedling survival.

The survival of seedlings was related to density. We used the log<sub>10</sub> mean densities of seedlings in the spring and seedling survival to autumn for each study area in 1985 and 1986 to estimate this relationship (Fig. 3B). From this relationship we determined the survival from seedling to the rosette stage in the model (Fig. 2). A lower limit of 1 % seedling survival was used in the model to prevent negative values.

## 3. Rosette survival.

Survival of rosettes and flowering plants over the summer was high, average 95%, and survival of rosettes was not related to density (Fig. 3C). Overwinter survival of rosettes is high (>99%) (Powell 1989) and was not considered in the model. Diffuse knapweed plants spend variable times as rosettes and we have used an average of 3 years for the persistence of this life stage (Powell 1988). Therefore the total survival for rosettes to the flowering stage is approximately 85%. A constant of 85% survival between the rosette and flowering stages was used for all plant densities.



#### 4. Seed production.

Seed production of flowering plants was related to plant density (Fig. 4). Data from the Cache Creek site were not included in this relationship because plants were both small and sparse at this particularly dry area and did not fit the relationship of the other sites that were more similar in their characteristics (see Tab. 1). The parameters of the relationship between plant density and seed production (slope and intercept) can be varied in the model. Two relationships are shown in Fig. 4. One is based on data from 4 sites and includes seed production per flowering plant for the Grandforks site in 1987, a year after it was burned. Burning reduced the density of plants to a low level and seed production was very high the next year. The other relationship excludes this out lying data point. In addition a hypothetical relationship was used which had a lower slope and intercept (Fig. 4).

#### 5. Final seeds.

Final seed production for the next iteration of the model was determined from the number of flowering plants and the production of seeds per plant calculated from one of the relationships in Fig. 4.

#### 6. Biological control agents.

The impacts of biological control agents were considered in the following manner:

No agents: Since gall flies were established at all sites at the time of this study, we needed to correct for seed loss by fly attack in order to estimate conditions prior to biological control attempts. This effect was estimated from two values. Harris (1980b) compared seed production in areas with and without seed feeding flies and calculated that without gall flies seed production would be about 16.7 times higher than with flies. We calculated a lower value, 4.1 times, from taking the maximum number of seeds per seed head in knapweed seedheads with no flies (8.1 seeds) and comparing that to seed numbers in heads with fly galls (2.1 seeds). For the model we used a value that was intermediate between these two estimates, but biased toward the lower estimate of seed production, 8.3 times to be conservative. For runs of the model simulating no agents, total seed production was multiplied by 8.3 at the end of each iteration to adjust seed production to levels expected before the biological control program.

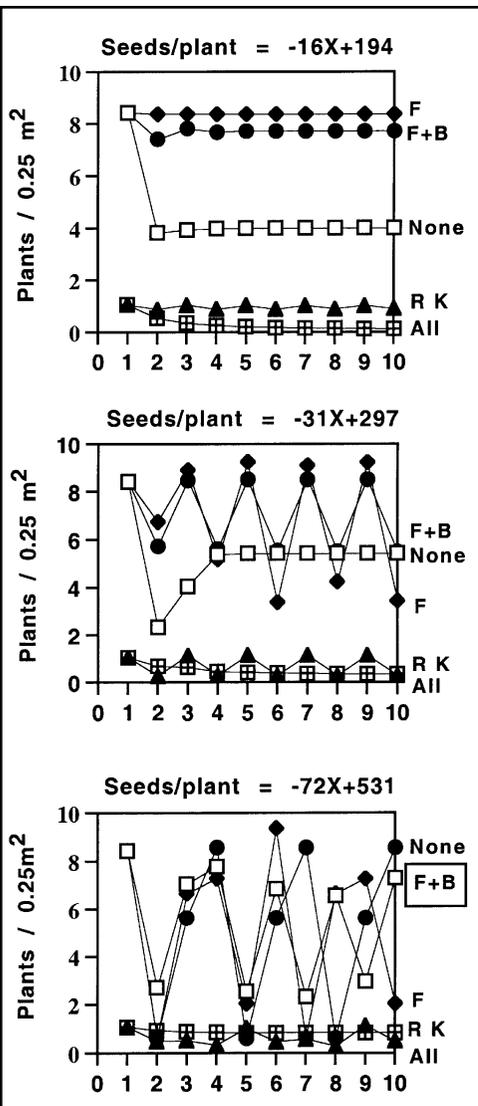


Fig. 5. Mean number of flowering plants per 0.25 m<sup>2</sup> for simulations using three different relationships between density and seed production per plant. Top - seeds/plant = -16x +194, middle - seeds/plant = -31x +297 and bottom seeds/plant = -72x +531. F= flies, F+B= Flies + Beetles, RK= rosette killer, None= no agents, All= all agents.

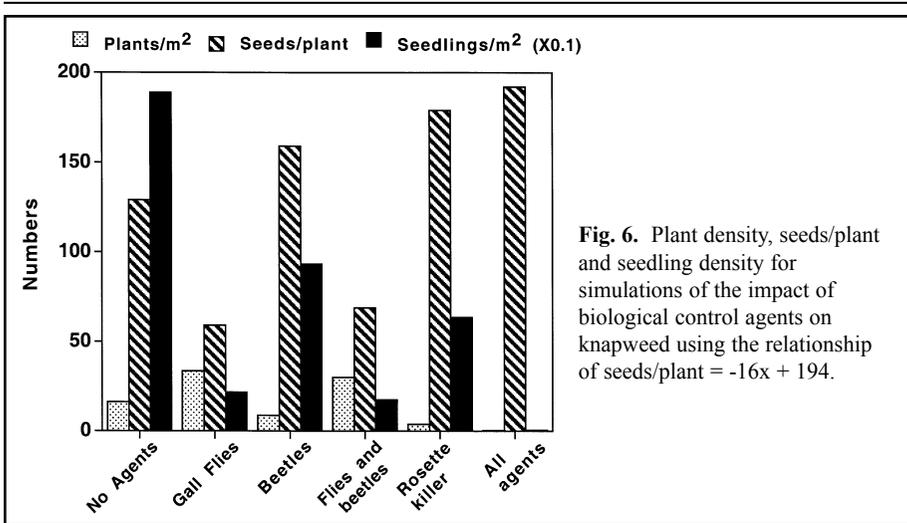
Gall flies - Since gall flies were established at all sites at the time of the study the relationships used in the model incorporated the impact of these flies on seed density.

Root boring beetle - Between 1978 and 1986 beetles were found in an average of 65% of all flowering plants at the White Lake site. Seed production is reduced by approximately 40% in plants attacked by beetles (Powell and Myers 1988). Seed production with beetles is therefore 0.74 of that in areas without beetles, (1 - (0.65 \* 0.4)).

Hypothetical rosette-killing agent - To explore the potential impact of an agent which kills knapweed plants we simulated a reduction in survival of rosettes to 50% a year over the average 3 year interval between maturation to the rosette stage and bolting of the rosette to the flowering stage. For these simulations total mortality changed from 85% based on annual rosette survival of 95% per summer, to 12.5%. In runs with only this agent seed production was corrected for seed loss by fly attack in the original data.

### Results

Densities of flowering plants for simulations using three different relationships for plant density and seeds per plant are shown in Fig. 5. Using the relationship with the lowest slope and intercept for the plant density - seed production relationship resulted in simulated populations rapidly reaching equilibria (Fig. 5). Reduction in seed production by flies alone or with beetles resulted in higher knapweed densities in these runs. Reduced survival of rosettes caused by a hypothetical rosette killer reduced plant density and a combina-



tion of all agents further reduced plant density. In simulations using a relationship between plant density and seed production based on field data and having an intermediate slope and intercept, the addition of gall flies alone or flies and beetles destabilized knapweed populations. Again the rosette killer reduced plant population density (Fig. 5). A steeper relationship between plant density and seed production further destabilized simulated populations and simulations of flies and flies with beetles were more variable among generations than simulations of control conditions without seed reduction. Again reduced survival of rosettes was translated into lower plant population density (Fig. 5).

The relationship between plant density, seeds/plant and seedlings/m<sup>2</sup> in simulated populations which reached equilibrium densities (Fig. 5) are shown in Fig. 6. For simulations of seed reduction by gall flies either without or in conjunction with beetle attack, seedling density was lower but flowering plant density was higher as compared to simulated populations lacking biological control agents. Densities of flowering plants in simulations were similar to mean densities observed in the field populations, 4.4 to 36 per m<sup>2</sup>. Mean densities of seeds per plant (42 to 792/plant) and mean numbers of seedlings per m<sup>2</sup> (124 to 7880) observed in field populations were also similar to the ranges of values from simulations.

## Discussion

The self-thinning principle is well known in plant ecology (discussion in Silvertown and Lovette Doust (1993)). High densities of seedlings are often reduced while at low density seedling survival can improve. This ability of plants to compensate for reduced seed production and for seedling survival to vary with plant density make achieving successful biological control of weeds difficult and results of biological control programs unpredictable. In an experimental study of the ability of diffuse knapweed to compensate for the removal of rosettes we found that removal of 40 and 80% of rosettes in the spring from two sites, Cache Creek and Buse Hill, was compensated for by increased development of

seedlings (Myers, *et al.* 1988). By autumn the densities of rosettes on removal plots were comparable to those of control plots. However, at a third site, White Lake, removal of rosettes significantly reduced plant density by autumn which indicates less compensation in this population. Figure 1 shows that density of knapweed at this site did not decline following an approximate 95% reduction in seed production following the establishment of gall flies and root boring beetles in the mid-1970's. Knapweed densities may however be more variable in recent years. This may be associated with a reduction in the seed bank or could have been influenced by rainfall patterns which explain 40% of the variation in plant density between 1978 and 1994. Increased variability was one of the outcomes of the simulated reduction of seed production in the study reported here and the model also lacked a seed bank. We did not incorporate compensatory survival of rosettes in the model, and killing rosettes was indicated by the simulations to be the only way to reduce knapweed density.

The conclusion that knapweed can compensate for reduced seed production agrees with the findings of Powell (1988). Furthermore these results show that to understand the impacts of biological control agents it is imperative that models incorporate the density related interactions which go on in populations. Using models such as matrix models which do not include density dependence (Cloutier and Watson 1990) will not allow realistic predictions of the outcomes of biological control programs (Myers 1992).

If plants survive less well and produce fewer seeds at high density than at low density, biological control agents which reduce seed production are unlikely to have a large impact on plant density. In fact, the simulations presented here indicate that in some situations reduced seed production may even increase plant density. The impact of insect herbivores on host plant dynamics will be determined by the ability of plants to compensate for reduced density at early life history stages. Successful biological control agents are much more likely to be those that kill plants. Some examples include the control of prickly pear cactus by *Cactoblastis* moth (Myers, *et al.* 1981), the control of tansy ragwort by the ragwort flea beetle *Longitarsus jacobaeae* (McEvoy, *et al.* 1993), and the control of water fern, *Salvinia molesta*, by the weevil *Cyrtobagous salviniae* (Room 1990). However, insects with the ability to kill their host plants might be rare in natural situations (Myers 1992).

Three additional species have been introduced on knapweeds in North America, a root moth *Agapeta zoegana*, a root weevil, *Cyphocleonus achates*, and a seed weevil, *Larinus minutus*. (Wikeem, *et al.* 1996, Wikeem, *et al.* 1999). The impacts of these have not been evaluated, but we predict that unless these insects are able to kill rosette plants they will not reduce knapweed densities. It is interesting to note that attack by the root moth, *Agapeta*, may increase the competitiveness of knapweed with grass and this demonstrates how an insect herbivore may exacerbate a weed problem (Callaway, *et al.* 1999).

One example in which a seed predator is considered to be a successful control agent involves *Rhinocyllus conicus* Froel. on nodding thistle, *Carduus nutans* L. (Harris 1984, Kok and Surles 1975). In both of these studies thistle density declined after beetles became established, but in neither case were control sites with similar aged infestations of thistles studied. Unlike diffuse knapweed which can invade sites with little disturbance (Myers and Berube 1983), the establishment of *C. nutans* is favored on disturbed sites (Wardle, *et al.* 1995). Once established it can dominate the site. Other plants may regain the competitive advantage when the seed production is reduced by *Rhinocyllus*. It is interesting that at one of the nodding thistle sites studied by Harris (1984), an unused gravel

pit, plant density varied from 8 to 19.9 plants per m<sup>2</sup> in the first 6 years following release of *R. conicus*, but in the next 6 years, after the beetles were established, plant densities varied from 0.4 to 52 plants per m<sup>2</sup>. This is consistent with destabilization of host plant densities by seed reduction shown in the simulations of knapweed populations (Fig. 5).

Nodding thistle also differs from knapweed by having lower survival of the rosette stage. Summer survival of rosettes of nodding thistle in its native habitat in France was approximately 30%, and in one summer was only 10% (Sheppard, *et al.* 1989). This is considerably lower than the survival of knapweed rosettes which we observed (95% per summer). If rosette survival is typically low for nodding thistle, this may explain the greater susceptibility of nodding thistle to reduced seed production.

In New Zealand *Rhinocyllus* did not reduce the density of nodding thistles. At one site seed production was reduced by 40% but according to Kelly and McCallum (1995) density-dependent survival from seedling to flowering plant ameliorated the seed loss. Recently Shea and Kelly (1998) estimated the potential impact of *Rhinocyllus* with matrix models. As mentioned above, matrix models which do not include density-dependent survival relationships overlook potentially important compensatory relationships and therefore are not realistic (Myers 1992). However, the matrix model of Shea and Kelly indicated that without any consideration for compensation for reduced seedling density, approximately 69% of the seed would have to be removed by *Rhinocyllus* for the population to decline. This can be compared to the 81-99% seed reduction by a combination of seed predators in native nodding thistle populations in Europe (Sheppard, *et al.* 1994). Elasticity analysis of the model showed that seed to seedling and small plant/seed transitions were more important than rosette survival in determining population growth of nodding thistles in New Zealand.

Yellow star thistle, *Centaurea solstitialis*, is another system for which 6 seed feeding agents have been introduced and have become widely established (Pitcairn, *et al.* 1999). Although seed and seedling production have been reduced in the 5 or 6 years since the introduction of the agents, no reduction in adult plant density has been observed. Since this plant is mostly an annual, reduced adult plant densities should reflect reduced seedling densities almost immediately unless there is continued self-thinning of seedlings. No studies have been reported that measure density-related seedling survival for this species. Measuring the level of attack is not a measure of biological control success for this and other exotic knapweeds.

That seed predators may influence the recruitment and density of a native thistle was shown experimentally by Louda and Potvin (1995). Exclusion of inflorescence-feeding insects from *Cirsium canescens* with insecticides increased flowering plant density. This suggests that the relationships between seed production and plant density might be different for native, non-weedy thistles and exotic, weedy thistles.

The population dynamics of another weed that has been modeled is scotch broom, *Cytisus scoparius* (Rees and Paynter 1997). These models predict that herbivores that reduce plant fecundity could reduce broom density when the disturbance rate is high, plant fecundity is low and seedling survival is low. Unfortunately these are not characteristics of introduced populations of broom. In Oregon an 85% reduction in broom seeds by *Exapion fuscirostre* did not reduce broom density or slow its spread (Andres and Coombs 1992). Following an analysis of broom populations in Australia and New Zealand, Paynter *et al.* (1996) concluded that "introduced seed-feeders are unlikely to reduce populations of broom" (p. 500) although they speculated that high seed predation might slow the rate

of invasion. The important factor is how much of the spread of the weed is by diffusion of seeds from established sites and how much is long distant movement of plants and seeds associated with chance events. For broom, seedling density is only very weakly related to the density of seeds in the seed bank in undisturbed sites (Fowler, *et al.* 1996). This suggests that seedling establishment is limited by the number of "safe sites" for germination rather than seed production (Andersen 1989).

Louda (1982a, 1982b, 1983) studied the impact of seed predation on two closely related, native shrubs, *Haplopappus squarrosus* H. and A., and *H. venetus* Blake over a climatic gradient in southern California. She found that in *H. venetus* reduced seed predation was translated into increased seedling establishment at a coastal site, but not at an inland site. Unmanipulated plants on the coast had twice the seed production of inland plants, but the density of flowering plants in the two areas was the same. For this species therefore seedling mortality is more important than seed production in determining plant density. This contrasts to *H. squarrosus* for which juvenile recruitment was determined by seed production and seed predators played an important role in determining population recruitment.

The crux of interpreting plant population regulation and the potential impact of herbivores on plant populations lies in the ability to identify and measure density-dependent relationships. But this can be confounded by year to year variation in weather and site to site variation in microclimate (Antonovics and Levin 1980). Measuring density as the number of plants per area gives only a crude estimate of intraspecific competition, an important aspect of the variation in plant performance, because the distribution of plants is not taken into account (Mitchell-Olds 1987, Powell 1989, Silander and Pacala 1985). Correlating survival measurements to density contravenes the assumptions of statistics since the density of plants contributes to both the dependent and independent variables (Hassell 1985, Weller 1987). A better, but more labor intensive approach is to monitor the survival of individual plants. While the relationships determined from field studies must be viewed as being approximate, and probably underestimate the true relationship, they do allow a start toward the analysis of the impact of insect herbivores, particularly seed feeders on plant density.

For many exotic weeds biological control provides the only possibility for long term reduction of plant density. However, the introduction of each new agent comes with the potential for indirect or non-target effects (Cory and Myers 2000) and therefore the decision to introduce an agent should include an evaluation of its potential effectiveness. Whether seed predators are likely to be effective biological control agents or if they reduce the spread of weeds sufficiently to justify adding another exotic species to a native environment is controversial. It is a sobering message that the one species of seed feeding insect that has apparently been a successful control agent, *R. conicus*, has also been the focus of attention for its potential impacts on native thistles (Louda 1998, Louda, *et al.* 1997). The message from the study of diffuse knapweed seems to be that insects that reduce seed production are not a good bet for biological control of invasive plants with high seed production, a characteristic of many exotic weeds.

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