The Functional Forms of Density-Dependent Birth and Death Rates in Diffuse Knapweed (*Centaurea diffusa*) Explain Why It has Not Been Controlled by *Urophora affinis*, *U. quadrifasciata* and *Sphenoptera jugoslavica*

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Abstract

The two tephritid flies *Urophora affinis* and *U. quadrifasciata* have greatly reduced the seed output of diffu
knapweed *Centaurea diffusa* in Canada. The buprestid beetle *Sphenoptera jugoslavica* has decreased seedli
and rosette survivorship rates, delayed flowering and further reduced seed output. While the combin
effects of these three insects have significantly reduced the knapweed population's potential growth rate, th
have not brought it under control. An examination of the functional form of density-dependent birth a
death rates in the knapweed population explains this weed's resilience to our current biological conti
introductions and suggests what will be required to control it.

Introduction

Three insect species introduced as potential biological control agents for diffuse knapweed British Columbia have now been studied sufficiently to evaluate the damage they inflict c the knapweed population. The two flies, *Urophora affinis* Frauenfeld and *U. quadrifascia* (Meigen) (Diptera: Tephritidae), maintain consistently high population numbers and togeth reduce the seed output per plant by 80 to 95% (Harris 1980, Roze 1981, Morrison 1987). Tl beetle *Sphenoptera jugoslavica* Obenberger (Coleoptera: Buprestidae) reduces seed output t a further 40 to 65% in the plants it attacks (Harris and Myers 1984, Powell and Myers 1988 Despite large fluctuations in the beetle population (Powell and Myers 1988) owing to i vulnerability to poor oviposition conditions related to weather (Zwölfer 1976), the proportic of flowering plants damaged by the beetle has grown quite steadily since its introduction its present level of 70 to 90% (Powell and Myers 1988). All of this damage is encouragin of course, but the practical success of any biological control program depends on reducing tl target population densities below some desired level based on an economic criterion. He the empirical record is not so encouraging. C. Risley and J.H. Myers (pers. comm., 198 found no decrease in the density of flowering plants at four sites where the two tephritid fli are established, and at White Lake, where the beetle is also established.

Some caution is warranted in interpreting these results at face value for two reasons. Fir the sample sizes at the monitoring sites were not sufficient to detect the modest decline density we anticipate on the basis of intensive local demographic studies (Powell and Mye 1988) against extensive spatial variance in population density (Powell, unpubl. dat: Second, the number of flowering plants tends to remain relatively constant despite changes mature plant density because the proportion of the population flowering is inversely related density (see below). Thus constancy in the number of flowering plants does not imp constancy in the population density.

Annual censuses of marked plants in permanent quadrats at White Lake between 1982 ar 1985 showed a steady decline in rosette densities, while the number of flowering plan remained stable (Powell, unpubl. data). Intensive observations on marked and mapp individuals in 1985 confirmed that recruitment of new rosettes failed to keep pace wi rosette mortality and flowering plant mortality. Overall, the population declined 14.3% th

year. It would be a mistake to claim, on the basis of these observations, that diffuse knapweed is declining throughout the White Lake basin. Indeed we know that it is not. Fig. 1 plots the numbers of mature plants in 24, 0.5 m² quadrats, in late September 1985 *vs.* the corresponding numbers in April of the same year. The densities declined in 17 of the 24 quadrats, including all of the higher density quadrats, remained constant in 2, and increased in 5 quadrats with densities below 100 plants/m². This pattern of simultaneous decline at high densities and increase at low densities means that the knapweed population is converging on a lower equilibrium density in the presence of the three biological control insects.
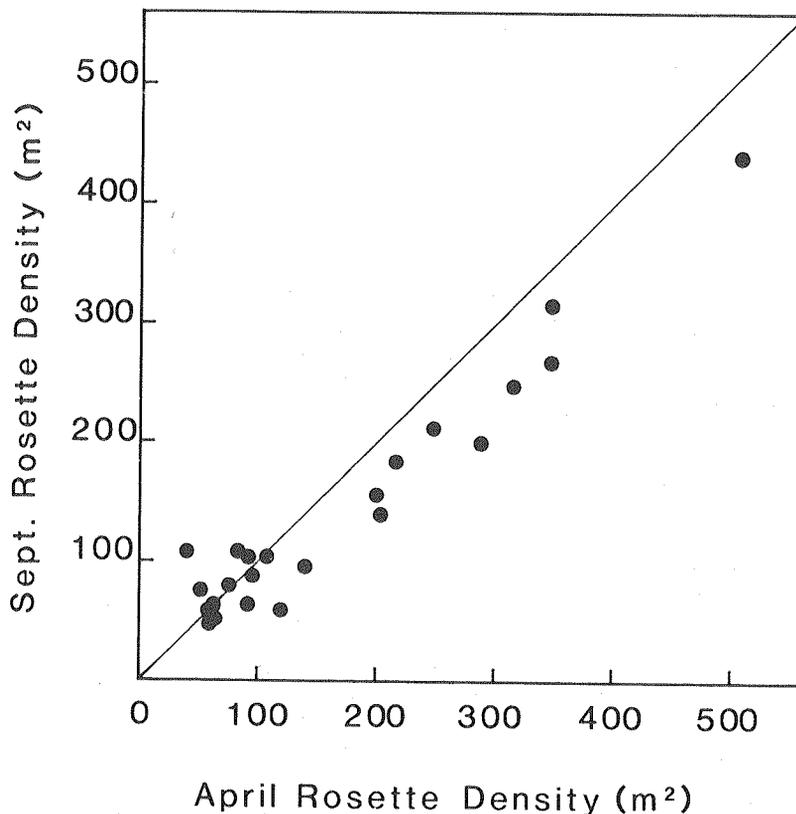

Figure 1. The change in knapweed numbers at White Lake in 1985. The densities of mature plants at the end of the growing season are plotted against the corresponding densities in the spring. Since winter mortality of rosettes is < 1%, the September numbers only slightly underestimate densities of the following spring.

The prospects for an increase in the density and biomass of displaced forage species depend on how low the density of knapweed will fall. It is possible to estimate the anticipated equilibrium density of the knapweed population at White Lake with data currently available, but this estimate cannot be used to gauge the expected densities at other infested sites. C. Risley and J.H. Myers (pers. comm., 1988) have shown that rates of seed production and mortality vary widely between sites. In contrast, the small repertoire of compensatory density-dependent responses that allows knapweed to persist despite the increased mortality and decreased seed output at White Lake will be common to knapweed at all sites. The shape of the density-dependent birth and death rate functions should therefore be qualitatively consistent between sites despite quantitative differences except, possibly, where other plant species are significant competitors. An examination of the shapes of density-dependent birth and death rates at White Lake reveals the mechanism which allows the knapweed population

to compensate for the damage inflicted by the three biological control agents, and suggests what will be required to overcome it.

Methods

The Birth Rate, Death Rate, and Equilibrium Density

Among the methods available for building simple population balance models capable of answering the above questions, I have chosen to begin with a form of the tautology that specifies additive components of population change; i.e., next year's population is this year's plus births minus deaths. This approach avoids the trap of adopting hidden assumptions such as linear density dependence in well-known formulas such as the logistic, without first assessing whether such simplifying assumptions are warranted (Walters 1986).

Fig. 2 is a schematic diagram of the life cycle of diffuse knapweed. There are exceptions, including fall germination (< 5% at White Lake), and iteroparity (about 2%), but the majority follow this relatively simple semelparous perennial life cycle. Following the synchronous spring germination, the population consists entirely of rosettes, R_t, and new seedlings, S_t. A proportion, f, of the rosettes will bolt in June, and flower in the summer. Almost all of these plants die in the fall, so the post-flowering mortality rate, q_f, approaches unity. The remaining $(1 - f)$ rosettes will persist in the vegetative state, and of these some fraction, q_r, will die. A fraction, q_s, of seedlings will also die, leaving $(1 - q_s)$ survivors to recruit into the rosette population.
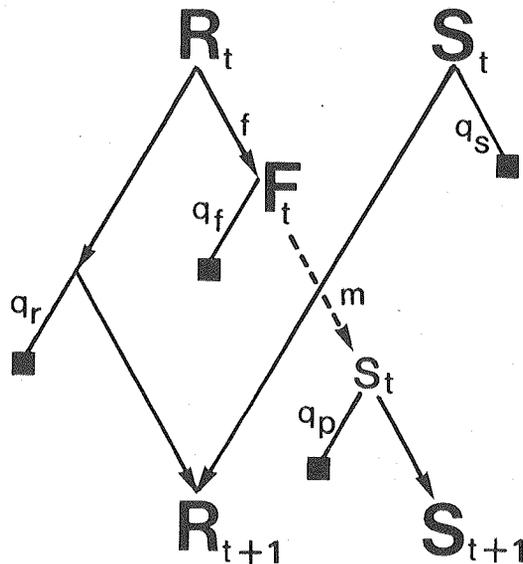

Figure 2. Schematic diagram of diffuse knapweed's life history. R, F, S and s represent numbers of rosettes, flowering plants, seedlings, and seeds respectively. Solid arrows indicate survival, the dashed arrow reproduction, and lines to solid squares indicate sources of mortality of seeds (q_p), seedlings (q_s), rosettes (q_r), and flowering plants (q_f).

From Fig. 2, it follows that the population difference equation is:

$$R_{t+1} = R_t (1 \cdot f)(1 \cdot q_r) + S_t (1 \cdot q_s) \tag{1.1}$$

or,

$$R_{t+1} = R_t (1\text{-}f)(1\text{-} q_r) + R_{t\text{-}1} fm (1\text{-} q_p)(1\text{-} q_s) \qquad (1.2)$$

The terms on the left of the + signs represent surviving rosettes; the terms on the right represent seedlings recruiting into the rosette population. The birth rate, defined as the rate of recruitment into the rosette population is:

$$b = \frac{S_t (1\text{-}q_s)}{R_t} \qquad (2)$$

The death rate is the sum of pre- and postreproductive mortality:

$$d = (1\text{-}f) q_r + fq_f \qquad (3)$$

where q_f is approximately equal to 1.0.

Each of the rate variables in these equations is potentially dependent on population density. To estimate the equilibrium population density we need to know how the three rate variables q_s, q_r and f, and seedling density, S_t, are related to the mature plant density, R_t. The equilibrium density is found where the birth and death rate functions intersect.

Data Acquisition and Analysis

All data were obtained between 1982 and 1985 at the primary release site of *S. jugoslavica*, White Lake British Columbia, because it was the only location where all three insects were present when this study began. Rosette and seedling mortality rates were obtained from 24, 0.5 m^2 quadrats, of marked and mapped plants in a study of rosette growth in relation to individual crowding (Powell, unpubl. data). The 971 rosettes and 1729 newly-germinated seedlings inside the quadrats were individually labelled in early April 1985 (detailed methods in Powell 1990). The survivors and tags of dead plants were collected in late September 1985, and the proportion of seedlings and rosettes dying were calculated. There is almost no winter mortality of rosettes at White Lake; only four plants among 750 overwintering rosettes died in three winters (Powell and Myers 1988), so the number of rosettes in late September, both persisting and newly recruited, is a good estimate of their numbers in the following spring. The mortality rates observed between early April and late September only slightly underestimate annual mortality rates. The proportion of mature plants flowering was also observed in these quadrats, as well as 48, 0.5 m^2 quadrats, sampled in 1982. The numbers of seeds per plant were counted for all flowering plants in 11 m^2 quadrats including five where knapweed densities had been reduced by a herbicide (picloram; 4-amino-3,5,6-trichloropicolinic acid) 3 yrs prior to sampling.

All regressions on rosette density were fit by simple least squares. The three rate variables q_r, q_s and f, calculated as proportions dying and flowering, respectively, were arcsine transformed. Both variables were log transformed in the regression of seedling density on rosette density.

Results

The equations and summary statistics of the regressions are compiled in Table 1.

Fig. 3 shows the dependence of the four variables on rosette density. The dashed lines are 95% confidence intervals for the regressions.

Seedling mortality (3A) is consistently high at all rosette densities, and the slope of the regression through the data was not significant, ($P > 0.05$) suggesting that seedling mortality is independent of rosette density. However, this result depends heavily on the observed value at the one very high density quadrat. When that point is removed, the regression is highly significant ($P < 0.005$), which would agree with a separate analysis showing that seedling mortality is inversely proportional to the distance from the nearest rosette ($P < 0.005$).

Table 1. Summary statistics and regressions.

	Regression equation	r^2	df	F	Significance
f	$= sin(0.669 - 0.0011 R_t)^2$	0.475	(1, 67)	60.7	$P < 0.001$
q_r	$= sin(0.115 - 0.0007 R_t)^2$	0.21	(1, 22)	5.785	$P < 0.05$
q_s	$= sin(1.322 - 0.00037 R_t)^2$	0.13	(1, 22)	3.189	$n.s.$
$log_{10} s$	$= 3.709 - 0.008 R_t$	0.27	(1, 27)	9.85	$P < 0.005$
$log_{10} s$	$= 1.901 - 0.0031 R_t$	0.004	(1, 171)	0.659	$n.s.$
$log_{10} S_t$	$= 3.671 - 0.613 log_{10} R_t$	0.594	(1, 22)	32.21	$P < 0.001$

Rosette mortality (3B) is low, particularly below about 100 plants/m², where there was no mortality in 8 of 12 quadrats.

The proportion of mature plants flowering (3C) declines with density from about 1/3 to less than 1/20 ($P < 0.001$). This is expected because crowding at higher densities significantly slows rosette growth rates and prolongs the time a rosette needs to reach the flowering size threshold (Powell 1990).

The log of seedling density is inversely proportional to the log of rosette density (3D). The shape of this relationship is affected by the number of flowering plants in the previous year, their seed output, and the proportion of seeds that survive to germinate; from Fig. 2, $S_t = R_{t-1} fm (1 - q_p)$. The relationship between seed survival and mature plant density is unknown, although we do know that few viable seeds can be found in late summer (J.H. Myers, pers. comm., 1988). While the proportion of plants flowering is a decreasing function of density (3C), the number of flowering plants ($R_{t-1} f$) is not. The seed output/plant, m, shown in Fig. 4, has the required shape, and may be largely responsible for high densities of spring seedlings in quadrats with low mature plant densities.

The Equilibrium Population Density

Fig. 5 shows the birth rate and death rate functions obtained by substituting the regressions of rate variables into equations 2 and 3. The intersection of the two curves suggests an equilibrium density of about 70 plants/m², but no meaningful confidence interval can be estimated without further data to assess year-to-year variation in the birth and death rate curves. The value obtained should therefore be regarded as a "ballpark" estimate.

More interesting are the qualitative shapes of the curves. Clearly it would have been a mistake to assume linear dependence of birth and death rates on density; the logistic form would not be appropriate. The birth rate is concave, declining at a decreasing rate with density. The death rate, being the sum of prereproductive mortality that increases with density and post reproductive mortality that decreases with density (equation 3), is also shallowly concave. The per capita population growth rate is the difference between the two curves, $r = b - d$, and it too is concave. The implications of this observation are discussed below.
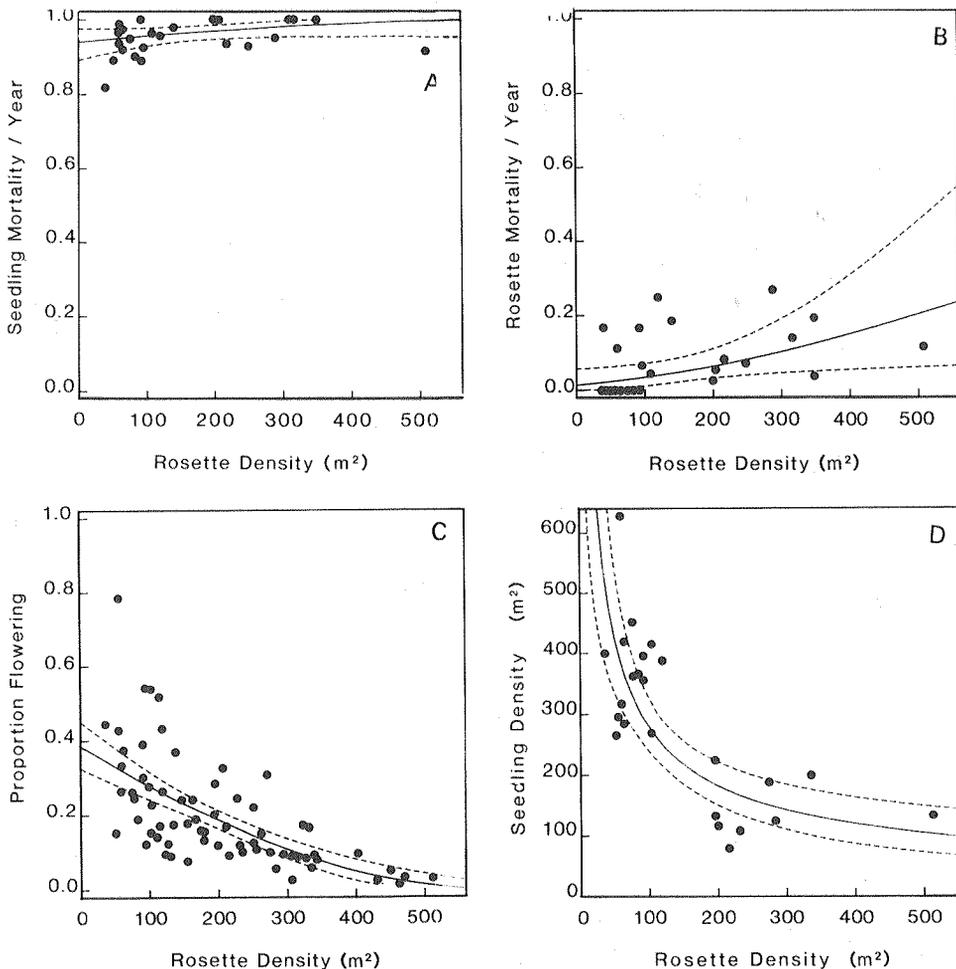
Figure 3. Regressions of the rate processes needed to calculate birth and death rates.

Discussion and Conclusions

Diffuse knapweed appears to be quite resilient to the combined damage caused by the three biological control agents *U. affinis*, *U. quadrifasciata* and *S. jugoslavica*. This can be explained in part by the shape of the per capita population growth rate curve. If it were convex, successive decreases in the birth rate or increases in the death rate due to new biological control introductions would lead to successively larger decreases in density. The increasing sensitivity of the population to small changes in birth and death rates would make it likely that a new agent would have a dramatic effect. Since the per capita population growth rate is instead concave, successive reductions in the birth rate or increases in the death rate will yield diminishing reductions in density. As long as the per capita population growth rate is concave, an abrupt decline in density is therefore unlikely.

The rough estimate of the equilibrium density for White Lake is probably not low enough to spark a dramatic increase in forage biomass; some quadrats already at that density have shown no sign of recovery. The further reductions in density we require can be obtained without attempting to alter the shape of the population growth curve, but each successive decline will require more damage, probably at increasing cost. An alternative is to look for ways to alter the odds. One way to do that is to select insects that preferentially damage the larger, more prostrate and faster-growing plants that are most common at lower densities.
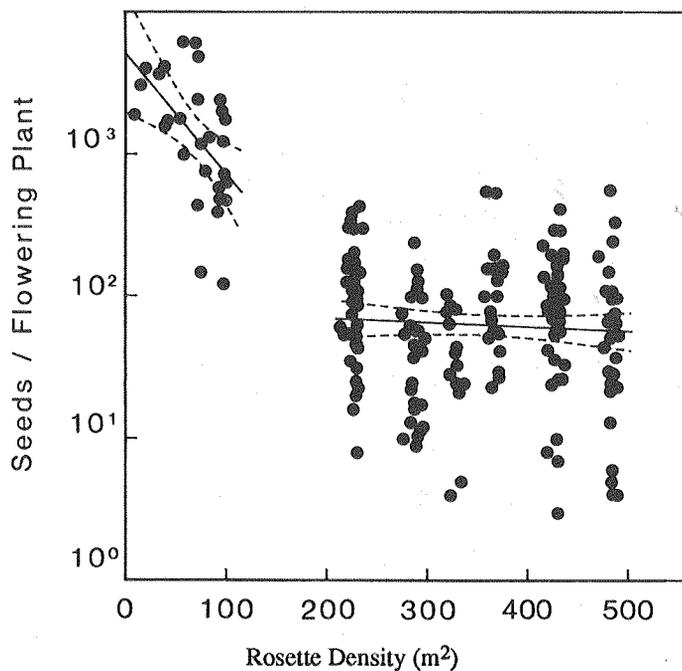
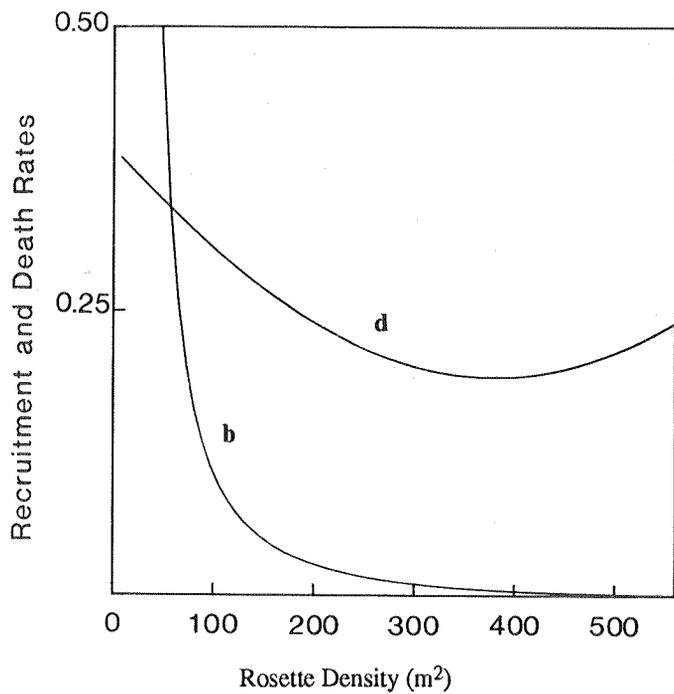**Figure 4. Seed output/flowering plant as a function of density.**

Figure 5. Birth and death rate functions.

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