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## Consumer pressure, seed versus safe-site limitation, and plant population dynamics

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**Abstract** Plants often suffer reductions in fecundity due to insect herbivory. Whether this loss of seeds has population-level consequences is much debated and often unknown. For many plants, particularly those with long-lived seedbanks, it is frequently asserted that herbivores have minimal impacts on plant abundance because safe-site availability rather than absolute seed number determines the magnitude of future plant recruitment and hence population abundance. However, empirical tests of this assertion are generally lacking and the interplay between herbivory, spatio-temporal variability in seed- or safe-site-limited recruitment, and seedbank dynamics is likely to be complex. Here we use a stochastic simulation model to explore how changes in the spatial and temporal frequency of seed-limited recruitment, the strength of density-dependent seedling survival, and longevity of seeds in the soil influence the population response to herbivory. Model output reveals several surprising results. First, given a seedbank, herbivores can have substantial effects on mean population abundance even if recruitment is primarily safe-site-limited in either time or space. Second, increasing seedbank longevity increases the population effects of herbivory, because annual reductions in seed input due to herbivory are accumulated in the seedbank. Third, population impacts of herbivory are robust even in the face of moderately strong density-dependent seedling mortality. These results imply that the conditions under which herbivores influence plant population dynamics may be more widespread than heretofore expected. Experiments are now needed to test these predictions.

**Key words** Herbivory · Plant population dynamics · Seed- versus safe-site-limited recruitment · Seedbank · Simulation model

### Introduction

Herbivorous insects are ubiquitous, and their interactions with host plants are well chronicled. Yet despite a voluminous literature on plant-insect interactions, the effects of these consumers on plant population dynamics remains uncertain (Hunter 1992) and much debated (Hairston et al. 1960; Jermy 1984; Andersen 1989a; Crawley 1989a, 1990, 1992; Hairston and Hairston 1993; Jermy 1993; Louda 1995; Louda and Potvin 1995). Both low-density populations and consumption of only a small fraction of net primary productivity have historically been taken as *prima facie* evidence that insect herbivores seldom regulate plant populations (Hairston et al. 1960; Jermy 1984; Crawley 1989a, 1989b; Crawley and Pacala 1991). Perhaps due to this perspective, population-level studies on plant-consumer dynamics have mostly focused on consumer rather than plant populations. While research has examined whether consumer populations are regulated by natural enemies (top-down regulation) or by the quality or quantity of plant resource (bottom-up regulation) (reviewed by Hunter 1992), few studies have focused on whether consumers themselves limit native plant populations (but see Louda and Potvin 1995; Carson and Root 2000 for notable exceptions).

A common demographic route by which insect herbivores influence plant performance is by reducing seed production. While a large number of experimental studies have documented such effects (Waloff and Richards 1977; Louda 1982a, 1982b, 1983; Hendrix 1984; Auld 1986; Auld and Myerscough 1986; Zammit and Hood 1986; Andersen 1988, 1989b; Evans et al. 1989; Louda 1989; Louda and Potvin 1995; Wise and Sacchi 1996; Maron 1998), how these rather common herbivore-driven reductions in seed output affect future abundance

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and population dynamics of plants is still mostly a mystery. Of the hundreds of studies that have documented negative effects of consumers on plant performance, only a few have determined whether these effects have population-level impacts. Results from these exemplary studies have shown that for plants with transient or no seedbanks, herbivory that lowers seed production reduces the number of individuals that recruit into populations, ultimately affecting adult plant abundance (Louda 1982a, 1982b, 1983; Louda and Potvin 1995). Based on these results, Louda and Potvin (1995) predicted that population-level effects of consumers on plants are most likely to be manifest in fugitive species where recruitment is tightly linked to current seed rain.

In contrast, it is often thought that plant populations that recruit from abundant seedbanks (and therefore lack a strong link between recruitment and current seed rain) seldom suffer negative population impacts of seed predation (Harper 1977; Andersen 1989a; Crawley 1989a, 1992). The reasons for this are twofold. First, recruitment into plant populations may be limited by safe-site availability rather than absolute seed abundance. According to this argument, if superabundant seeds fill all potential safe-sites, any additional seeds produced will have no effect on the magnitude of recruitment. Even heavily attacked plants with lowered seed output may still produce more than enough seeds to fill all available safe-sites. In this case, herbivore-driven reductions in seed production will have minimal impacts on future plant abundance. Second, density-dependent seedling survival can be compensatory. That is, even if reduced seed production limits seedling establishment, increased survival of seedlings growing at low density can compensate for this decrement in recruitment.

In the extreme and trivial case, plant populations that are always safe-site-limited, or those that always experience fully compensatory density dependence will be minimally affected by herbivores that reduce seed rain. However, many species are rarely always safe-site-limited; rather, they are safe-site-limited in some years or in some locations and seed-limited in others (Eriksson and Ehrlen 1992), depending on the size of the current seed crop, seedbank size, and variability in conditions that trigger germination. Also, density-dependent seedling mortality is unlikely to be always 100% compensatory. A more realistic scenario is that the strength of density dependence shifts over a range of conditions, from fully compensatory to partially compensatory, depending on both the initial density of seedlings and environmental conditions. A key to understanding the potential population impacts of herbivores is determining how herbivory and seedbank dynamics interact with spatio-temporal variability in the strength of these density-dependent processes to mediate the population response to herbivory.

We know of no empirical work on plants with seedbanks that addresses these issues. The classic experiment to determine whether plant recruitment is seed- or safe-site-limited has historically involved sowing different densities of seeds into plots and determining whether

this results in correlated increases in seedling density. However, results from these types of experiments have been mixed; some cases show increasing seedling recruitment at greater seed densities (Hawthorne and Cavers 1976; Fowler 1988; Peart 1989; Shaw and Antonovics 1986; Sheppard 1987; Eriksson and Ehrlen 1992), while other cases show no such relationship (Sagar and Harper 1960; Putwain et al. 1968; Symonides 1979; Gross 1980; Duggan 1985; Peart 1989; Eriksson and Ehrlen 1992). Seed addition experiments are often extremely sensitive to temporal and spatial scale (Eriksson and Ehrlen 1992). Additionally, there are methodological problems that potentially cloud their interpretation (Louda and Potvin 1995). Given these factors, and the small spatial scales and short time intervals over which most seed addition experiments are performed, it is not surprising that results have been inconsistent.

Here we use a simulation model to explore the range of conditions under which we might expect herbivores to have population-level effects on plants with long-lived seedbanks. Specifically, we are interested in determining how often (in time or in space) a population must be seed-limited for herbivore-driven reductions in fecundity to have population level effects. Also, it is of interest to understand how seedbank longevity interacts with spatial or temporal variability in seed-limited recruitment to mediate the population response to herbivory. Our model is not meant to be a substitute for an analytical or empirical examination of these issues. Clearly, this area is ripe for both such approaches. Rather, we use the simulation model to examine the interplay between spatially explicit processes such as seed dispersal close to the parent and local density dependence with stochastic processes such as germination and survival, which may vary at local spatial scales as well as across time. In particular, we ask how: (1) the frequency of seed-limited recruitment through time or in space, (2) the average half-life of seeds in the seedbank and (3) the strength of density-dependent seedling mortality modifies the population effects of herbivory.

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## Methods

### Model structure

We developed a simulation model that examines the effects of seed herbivory on the long-term population dynamics of an annual plant in a temporally and spatially stochastic environment. We modeled a plant population inhabiting a square grid composed of 400 cells. To avoid edge effects, the grid wraps around (i.e., a toroid), so that seeds deposited off one edge fall into cells on the opposite edge. Each of the small cells that make up the grid simulates a plot size of 1 m<sup>2</sup>, the scale at which we impose density dependence. Each cell may contain any non-negative whole number of adults, seedlings, and seeds. Within the grid, we simulated plant population dynamics in the presence or absence of pre-dispersal seed herbivores that decrease seed output but do not affect plant survival. Output from the simulation provides a forecast of the long-term effects of herbivory on adult plant abundance, seed abundance, population dynamics, and spatial distribution.

## Effects of herbivory on plant fecundity

The simulation starts with an average of three adult plants per cell, drawn from a Poisson distribution truncated at 10. These adults produce seeds and die. To capture stochastic variation in individual seed production, the model randomly draws the numbers of seeds that each adult produces from a Poisson distribution capped at 1,000 seeds per plant. We arbitrarily set mean seed production in the presence of herbivory at 100 seeds per plant. Changes in this baseline level of seed production do not qualitatively affect model results. To simulate the impacts of herbivory, we assumed that protecting plants from herbivory would increase the mean of this distribution by either 2 or 2.5-fold. Experimental studies where plants have been protected from single or multiple herbivores commonly report an increase in viable seed production by two-fold (Green and Palmblad 1975; Hendrix 1979; Louda 1982b, 1983; Louda and Potvin 1995; Wise and Sacchi 1996; Maron 1998), and sometimes much higher (Waloff and Richards 1977; J.L. Maron, J.K. Combs, and S.V. Louda, unpublished work). Given the empirical data, our parameter values for the effects of herbivory on seed production are likely to be conservative.

## Seed dispersal and dormancy

Two-thirds of the seeds produced by each plant fall within the cell in which they are produced and one-third of seeds are dispersed uniformly outward to the eight contiguous cells that immediately surround the cell containing the parent plant. The viability of seeds that do not germinate declines exponentially with a characteristic half life and whether or not a particular seed remains viable is determined by selecting a random number and performing a Bernoulli trial. This allowed us to explore how seed-bank longevity (ranging from long to very long-lived seeds) influences the population response to herbivory. We limited the upper bound of seed-bank half-life to 10 years, since even at this half-life, 10% of seeds in any given cohort are still viable 50 years later. Simulations revealed that the effect of reducing seedbank half-life was to mute the population response to herbivory (see Results). We arbitrarily set the lower bound of seedbank half-life at 6 years, since this overall effect of seedbank half-life is clearly illustrated over the range of half-lives we chose. In trial runs where we altered seedbank half-life over a wider range of values, the general pattern of effects were unchanged.

## Temporal and spatial variation in frequency-dependent germination

Any plant population response to seed predation will clearly vary between two extremes. At one extreme, seeds fill all safe sites, and therefore safe-site availability rather than absolute seed density limits recruitment. In this case, herbivores consume “surplus” seeds, there is no correlation between seed and seedling density, and the population impact of any herbivore that reduces fecundity is negligible (Crawley 1989a, 1992). At the other extreme, populations are always seed-limited and density-dependent seedling survival is not compensatory. In these cases, herbivore-driven reductions in seed production lead to declines in future seedling abundance and this translates into reduced adult population sizes for populations attacked by herbivores. We used the model to explore how the population response to herbivory changes in the parameter space between these two extremes.

Safe-site availability can be thought of as a random process that can vary on both temporal and spatial scales. To model temporal variation, we varied the probability that all cells in the grid experienced seed-limited recruitment in any given year (i.e., were safe-sites for germination). Thus, the model simulates “safe sites” that are 1 m<sup>2</sup> in size and multiple seeds were allowed to germinate in any given safe site. An average of 5.0% of viable seeds germinate in each cell; the model generates a random number and performs a Bernoulli trial to identify whether a given seed germinates or not. One can think of these safe sites as simulating disturbed

patches in nature, within which recruitment is seed-limited. This aspect of our simulation is similar to “disturbed sites” in the simulation of biocontrol on Scotch broom by Rees and Paynter (1997). More generally, years with seed-limited recruitment in our model simulate years when environmental events such as flood, fire, or high rainfall trigger episodic recruitment. During these years, seedling recruitment correlates directly with seed density. Clearly, if the population is seed-limited in every year, and density-dependent mortality is not 100% compensatory, reductions in seed production due to herbivory will translate to a reduced population abundance.

In years without seed-limited recruitment, the population is safe-site-limited. That is, seedling abundance correlates with the number of safe sites (or cells in the model) but not with the absolute number of seeds. In these years, individual cells can be thought of as “undisturbed” sites in which there is only limited recruitment, regardless of seedbank density. To simulate this, the model only germinates one viable seed per cell, regardless of seed density (so long as there is at least one viable seed per cell). These years with safe-site-limited recruitment can be viewed as the extreme counterpoint to seed-limited recruitment. We had the model only germinate one seed per cell in safe-site-limited years because we were interested in modeling a population that had low abundance during most years that were safe-site-limited but then experienced episodic pulses of recruitment. Given this structure, we used the model to ask whether the population consequences of herbivory might be detected even if the frequency of seed-limited recruitment is low. Here a large population effect is not a large difference in the population size due to herbivory in any given year, but a substantial effect of herbivory on population size when averaged over all years. In trial simulations where we germinated five seeds rather than one seed per cell during safe-site-limited years, the population size averaged over 50 years increased by approximately 2.5-fold, but the population impact of herbivory remained qualitatively similar to when only one seed was germinated per cell. If we germinated even more seeds per cell during safe-site-limited years, the average population size increased still further.

To examine how spatial as opposed to temporal variability in seed-limited recruitment affects dynamics, rather than changing the percentage of years in which seed-limited recruitment occurs, we altered the mean percentage of cells within any given year that could experience frequency-dependent germination. Thus, for spatial variability in germination, in each year, a Bernoulli trial was performed for each cell to identify whether that cell would experience seed-limited germination (in which an average of 5.0% of seeds germinate) or safe-site-limited germination (in which 1 seed per cell germinates).

## Density dependence

After germination, seedlings experience density-dependent mortality. We set seedling mortality by a logistic density-dependent function that puts a ceiling of 80 on the maximum number of seedlings that can survive per cell:

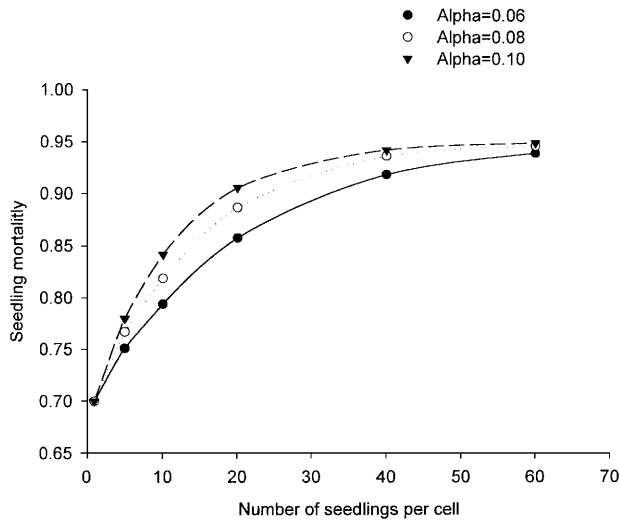
$$\text{Seedlings surviving per cell} = \min(80, \text{seedlings}) / \{a + (b - a) \exp(-\alpha \text{seedling number})\}$$

where  $a$  is the minimum seedling mortality, set at 0.7, and  $b$  is the maximum seedling mortality, set at 0.95. For the majority of model runs, we set  $\alpha$  in the above equation to 0.06, which produced reasonably strong density dependence (Fig. 1). However, to explore how increasing the strength of density dependence can potentially compensate for herbivore-driven reductions in seed production, we also ran the model with higher values of  $\alpha$ . As  $\alpha$  increases, the mortality fraction approaches the maximum value of 0.95 at lower numbers of seedlings (Fig. 1).

Despite high seedling mortality at high density, in seed-limited cells or years even a small fraction of seeds that germinate and survive to adulthood can produce an adult population size that is unrealistically large, given a large enough seedbank. To guard against unrealistically large population sizes that would bias simu-

**Table 1** Parameter values used in simulation

Parameters	Values used	Stochastic?
Seed germination	0.05	Yes
Seedling mortality (lower and upper bound)	0.70, 0.95	Lower bound – Yes Upper bound – No
Strength of density dependence ( $\alpha$ )	0.06, 0.08, 0.1	No
Mean seeds per plant (with herbivory)	100	Yes
Mean seeds per plant (without herbivory)	200, 250	Yes
Percentage of years (or cells) in which recruitment is seed-limited	10, 20, 30%	Yes
Seed viability (half-life)	6, 8, 10 years	No

**Fig. 1** Effect of the parameter  $\alpha$  on the strength of density-dependent seedling mortality

lation results, the model caps the maximum density of adult plants per cell at 80. If during any simulated year there are more than 80 adult plants per cell, those excess plants die before they set seed. For most combinations of parameter values, plant density never reached 80 per cell. The only set of parameter values that resulted in plant density occasionally reaching its cap occurred when populations were seed-limited 30% of the time (or 30% of cells) and plants produced an average of 250 seeds. However, even under these conditions, an average of only 13% of cells in any given year ever contained over 80 adult plants. We kept parameter values for germination percentage and the upper and lower bounds of seedling mortality constant across all model runs because changes in these values did not qualitatively influence model results.

#### Parameter values

Every year the simulation cycles from seed production and dispersal through adult mortality, seed germination, and seedling survival, yielding adult plants to begin the cycle again. If fewer than 200 seeds or 200 seedlings were present in a cell, then seed germination or seedling survival for each individual in that cell was simulated stochastically according to the probabilities described above. However, if more than 200 seeds or seedlings were present in a cell, then the fraction germinating or surviving was calculated deterministically, since the large numbers present make it unlikely that demographic stochasticity significantly affects population dynamics.

Table 1 summarizes the parameters in the model, and the range of values we used for each. Population dynamics were simulated for 60 years and replicated in 50 Monte Carlo iterations in the

presence or absence of herbivores. We averaged the numbers of seeds and adults across years 10–60 of each iteration, and then calculated the arithmetic mean of these values across iterations. We ignored data generated from years 1–10 since population sizes in these years were influenced by initial conditions. Since many of the parameter values were stochastic, separate iterations of the model simulate populations experiencing independent environmental conditions. Although population size was variable from year to year, under no set of parameter values was there a clear trend in population expansion or contraction through time that would be indicative of our not running the simulation for enough years.

We ran three sets of simulations. At first, we ran the model for the extreme case where herbivores should have maximal population impact: no seedbank and recruitment always seed-limited, and with  $\alpha$  set at 0.06. Under these conditions, the impacts of herbivory on population abundance should be great, because the link between seed production and seedling recruitment is tight. In subsequent runs of the model, we varied seed-bank half-life in the range of long-lived to very-long lived (a half-life of 6, 8, or 10 years) and explored how this, together with temporal or spatial variability in seed-limited recruitment, affected seedbank size and adult population size with and without herbivory. For these simulations we kept  $\alpha$ , the strength of density dependence, constant at 0.06. We performed separate *t*-tests to determine whether the decrease in mean population size due to herbivory was statistically significantly for each combination of parameter values for seedbank half-life and percentage of years (or cells) with seed-limited recruitment.

Finally, we varied the impacts of herbivores (using a 2.0- and a 2.5-fold increase in seed production), seedbank half-life (setting half-life equal to 6, 8, or 10 years), the strength of density dependent seedling mortality (setting  $\alpha$  equal to 0.06, 0.08, or 0.1), and temporal or spatial variability in seed-limited recruitment (with recruitment being seed-limited in 10, 20, or 30% of years or cells) using all combinations of parameter values to determine how these factors in isolation and jointly affected the population response to herbivory. We did not increase the fraction of time or space that seedling recruitment was seed-limited above 30% because unrealistically high population densities resulted. In total, we performed simulations for 162 unique combinations of parameter values. Within the bounds set on parameter values, the model produced a wide range of population sizes that amply illustrate the relative importance of seed- versus safe-site-limited recruitment, seedbank longevity, and density dependence. Increasing either the longevity of the seedbank and/or the number of years that populations experience seed-limited recruitment will only increase the expected population response to herbivory. Given the large number of parameter combinations that we used, we used a sensitivity analysis to quantitatively assess the relative importance of each parameter on mean population abundance and mean seedbank abundance (both variables log-transformed), respectively. To do this, we performed two four-way ANOVAs with herbivory, seedbank half-life, density dependence, and degree of seed-limited recruitment as dependent variables and determined the fraction of the total sum of squares (or interaction between parameters) accounted for by each parameter (see Doak et al. 1992 for a similar approach). Although the results of this analysis are influenced by the range of values



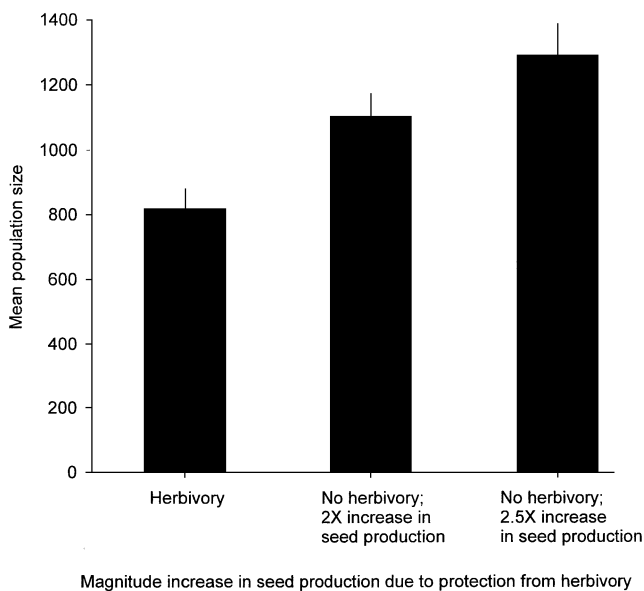
used for each parameter, the utility of this analysis is that it allows insight into the relative importance of different parameters under varying model conditions.

## Results

In simulations where recruitment was always seed-limited and there was no seedbank, populations that were free from herbivory produced more seeds, which led to greater seedling recruitment and significantly higher mean population size compared to populations exposed to herbivory. This is the outcome one would expect given seed-limited recruitment. Since the same percentage of seeds germinate regardless of seed density, greater seed production leads to greater seedling germination. However, the effect of herbivory on population size was relatively modest, given the 2-fold or 2.5-fold increase in seed production that resulted from herbivore protection. Simulated populations without herbivory were only 35% or 63% larger than populations exposed to herbivory, respectively (Fig. 2). The relative insensitivity of population size to differences in seed abundance and recruitment illustrates the compensatory nature of density dependence.

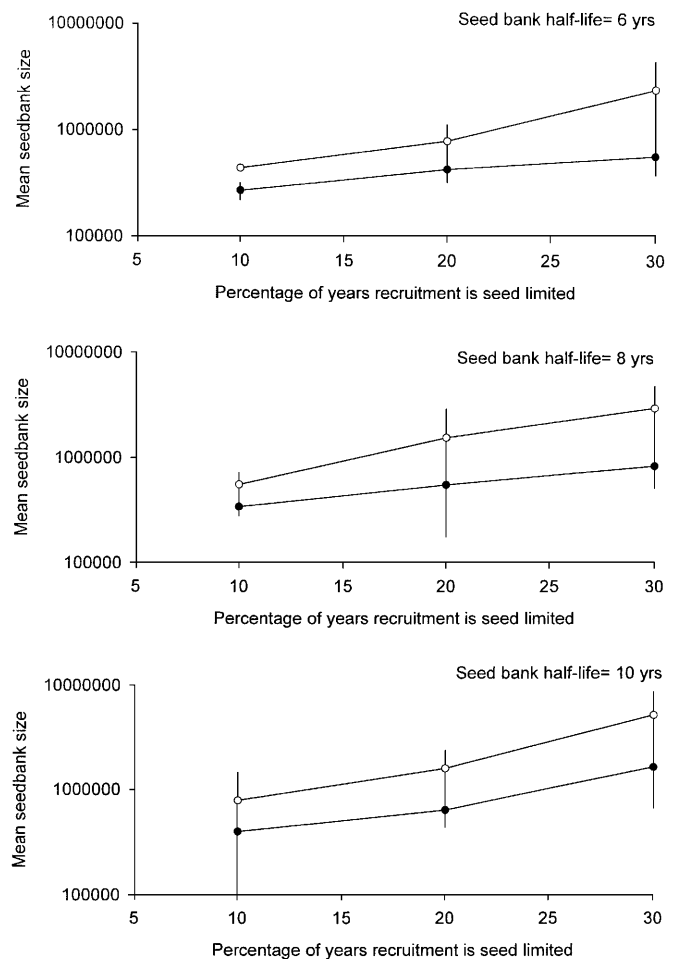
### Temporal variability in seed-limited recruitment

Under a range of parameter values, populations lacking herbivory had significantly larger seedbanks than did populations with herbivory (Fig. 3; separate *t*-tests for each comparison,  $P < 0.05$ ). A critical question concerns

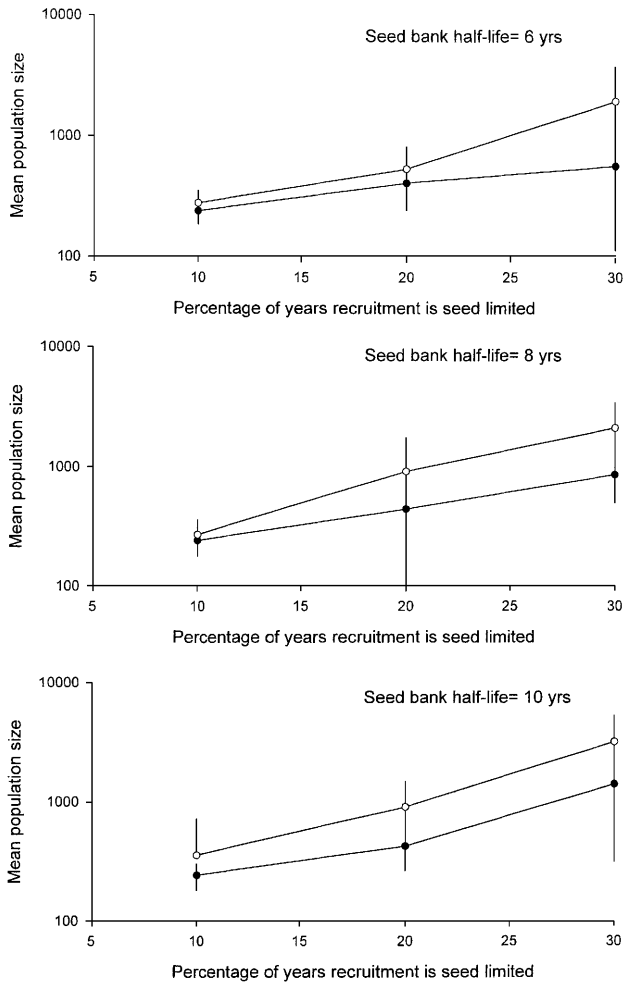


**Fig. 2** Mean ( $\pm 1$  SD) simulated population size averaged across 50 years with and without herbivory, in simulations run with no seedbank and seed-limited recruitment every year. Protection from herbivory increases average plant fecundity either 2-fold or 2.5-fold

the conditions under which these gains in seedbank abundance translate into increased adult abundance for populations protected from herbivory. As one might expect, as the number of years in which there was seed-limited recruitment increased, there were more opportunities for frequency-dependent germination from the seedbank, which enabled the effects of herbivory on seedbank size to be expressed at the level of the adult plant population (Fig. 4). Surprisingly, however, herbivory had large effects on population size, even when recruitment was seed-limited in a minority of years. When recruitment was seed-limited (and hence correlated to seedbank size) in only 20% of all years, a 2-fold increase in seed production due to the absence of herbivory resulted in a 31–136% increase in mean population size. Whether the population response was on the low side (i.e., a 31% increase over populations exposed to herbivory) or the high side (i.e., a 136% increase) depended



**Fig. 3** Effect of temporal variation in seed-limited recruitment and seedbank half-life on the impacts of herbivory on the seedbank. Mean ( $\pm 1$  SD) simulated seedbank size averaged across 50 years with (filled circles) and without (open circles) herbivory. Seedbank size in any given year is the sum of seeds in all 400 grid cells. The reduction in seedbank size due to herbivory is significant for each pair of means in each panel (separate *t*-tests for each comparison,  $P < 0.05$ )

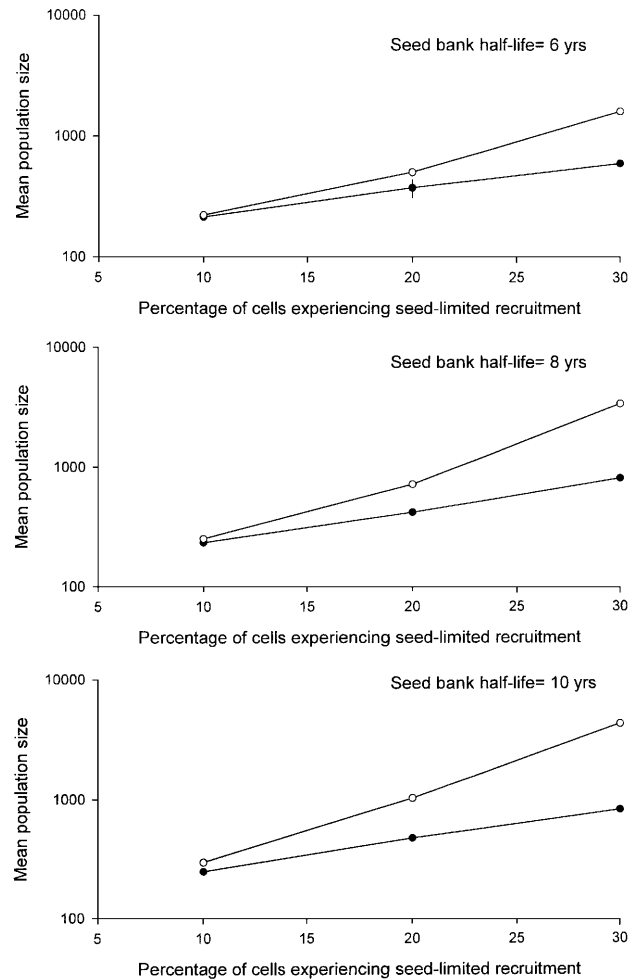


**Fig. 4** Effect of temporal variation in seed-limited recruitment and seedbank half-life on the population response to herbivory. Mean ( $\pm 1$  SD) simulated adult population size averaged across 50 years with (*filled circles*) and without (*open circles*) herbivory. Adult population size in any given year is the sum of adult plants in all 400 grid cells. The reduction in population size due to herbivory is significant for each pair of means in each panel (separate *t*-tests for each comparison,  $P < 0.05$ )

on the longevity of the seedbank (Fig. 4). As the residence time of seeds in the soil increased, the effects of herbivory on population size also increased. However, in all cases, herbivory caused statistically significant decreases in plant abundance (separate *t*-tests for each comparison,  $P < 0.05$ ).

#### Spatial variability in seed-limited recruitment

Within any given year, spatially altering the number of safe-sites in which seed-limited recruitment could occur produced qualitatively similar results as changing the frequency of seed-limited recruitment through time (Fig. 5). Predictably, as the percentage of cells that experienced seed-limited recruitment increased (and was held constant across years), the population response to herbi-



**Fig. 5** Effect of spatial variation in seed-limited recruitment and seedbank half-life on the population response to herbivory. Mean ( $\pm 1$  SD) simulated adult population size averaged across 50 years with (*filled circles*) and without (*open circles*) herbivory. Adult population size in any given year is the sum of adult plants in all 400 grid cells. The reduction in seedbank size due to herbivory is significant for each pair of means in each panel (separate *t*-tests for each comparison,  $P < 0.05$ )

vory also increased. Yet, here again, only a small fraction of cells needed to experience seed-limited recruitment for the impacts of herbivory to be substantial, despite the fact that seed rain was modeled to be predominantly local, making the seed population spatially clumped. When only 20% of available cells each year experienced seed-limited recruitment, protection from herbivory resulted in an increase in mean seedbank size between 91% and 171%. This gain in seed density translated to a 35–115% increase in plant abundance, depending on seedbank half-life (Fig. 5; separate *t*-tests for each comparison,  $P < 0.05$ ). At higher seedbank longevity, the population response to herbivory increased. When 30% of cells in any year experienced seed-limited recruitment, if the seedbank had a half-life of 10 years, the protection from herbivory resulted in a 3.2-fold increase in population size. Thus, given a long-lived seedbank, seed-

**Table 2** Relative effect of different model parameters in explaining variance in mean adult population size, mean seedbank size, and mean coefficient of variation in adult population size when seed-limited recruitment varied temporally. Each table entry is the percentage of total sum of squares explained by a given parameter in a four-way ANOVA. Main effects (or interactions) that explain

	Mean population size	Mean seedbank size	Mean coefficient of variation
Percentage of years recruitment is seed-limited	49.5%	35.0%	65.0%
Herbivory	16.5%	34.5%	–
Herbivory×seed limitation	5.1%	4.1%	–
Seedbank half-life	2.7%	6.6%	–
Strength of density dependence	–	–	–
Error	24%	18%	29.3%

**Table 3** Relative effect of different model parameters in explaining variance in mean adult population size, mean seedbank size, and mean coefficient of variation in adult population size when seed-limited recruitment varied spatially. Each table entry is the percentage of total sum of squares explained by a given parameter in a four-way ANOVA. Main effects (or interactions) that explain

	Mean population size	Mean seedbank size	Mean coefficient of variation
Percentage of years recruitment is seed-limited	65.3%	47.4%	46.9%
Herbivory	15.5%	27%	20.9%
Herbivory×seed limitation	9.7%	4.9%	11.5%
Seedbank half-life	2.5%	4.9%	–
Strength of density dependence	–	–	–
Error	5.2%	14.5%	13.5%

less than 2% of the total sum-of-squares are denoted with a *dash*. Interactions that are not listed in the table account for less than 1% of the total sum of squares in the response variable. Main effects in model are: percentage of years in which the population experiences seed-limited recruitment, herbivory, seedbank half-life, and  $\alpha$ , the strength of density dependence

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limited recruitment need only occur in a relatively small fraction of sites for there to be important population consequences of herbivory.

In addition to effects on population abundance, herbivory had strong impacts on the spatial distribution of the population. Protection from herbivory increased the coefficient of variation of population size, indicating that the simulated population became more spatially clumped in the absence of herbivory than with herbivory.

#### Sensitivity of results to parameters

We performed a sensitivity analysis to quantify the relative effects of the frequency of seed-limited recruitment, seedbank longevity, and density-dependent seedling mortality on the magnitude of the population response to herbivory. Population size was most sensitive to both the frequency of seed-limited recruitment and herbivory (Table 2). In isolation, the main effects of seed-limited recruitment and herbivory accounted for 66% of the variance in population size. Herbivory alone accounted for 16.5% of the variance in population size. When all combinations of parameter values were evaluated together and the frequency of seed-limited recruitment was varied in time, the herbivory by seed-limitation interaction accounted for 5.1% of the variance in adult population size. This indicates that the magnitude of the population response to herbivory varies as a function of the number of years the population is seed-limited.

Seedbank longevity had small but significant impacts on population size. Interestingly, density dependence had fairly minor impacts on population size, although this may simply reflect the narrow range over which we varied density-dependent mortality (0.70–0.95 mortality). The fairly large error term (accounting for 24% of the variance in population size) undoubtedly reflects the fact that the model has many stochastic elements. This points toward the potential difficulty of detecting population responses to herbivory in field experiments where environmental and demographic stochasticity might easily obscure detection of important population impacts of herbivory.

Similarly to adult population size, seedbank population size was also highly sensitive to herbivory and temporal variation in seed-limited recruitment (Table 2). Herbivory accounted for a much higher percentage of variation in seedbank size (34.5%) than it did in adult population size (16.5%). This is not surprising given that the link between herbivory (which reduces seed output) and seedbank abundance is more direct than the link between herbivory and adult population size. The average half-life of seeds in the seedbank accounted for 6.6% of the variance in seedbank size and the interaction between seed-limited recruitment and herbivory accounted for 4.1% of the variance in seedbank size.

The spatial coefficient of variation among cells of the number of plants was primarily sensitive to the proportion of years in which there was seed-limited recruitment (Table 2). The parameter  $\alpha$ , seedbank half-life, and her-

bivory accounted for very little of the variation in the mean coefficient of variation.

Variance components were similar when seed-limited recruitment varied spatially rather than temporally (Table 3). The three primary differences between them were that, first, the fraction of cells with seed-limited recruitment explained a greater proportion of variance than the corresponding temporal component of the percentage of years with seed-limited recruitment. Second, the error was much smaller with spatial than with temporal variation in germination. Finally, herbivory accounted for a much greater percentage of the variance in the spatial coefficient of variation among seed density in different cells given spatial versus temporal variation in seed-limited recruitment (Table 3).

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## Discussion

Many experimental studies now show that native insects can decrease native plant fecundity (Waloff and Richards 1977; Louda 1982a, 1982b, 1983; Auld and Myerscough 1986; Louda and Potvin 1995; Root 1996; Maron 1998). However, how these reductions in fecundity translate across generations to affect plant population abundance is almost entirely unknown, particularly for plants with persistent seedbanks.

It is often asserted that consumers have minimal effects on the abundance of plants with large seedbanks because “seed limitation may be the exception rather than the rule” (Crawley 1992). Moreover, even when local seed density is correlated with seedling density, density-dependent seedling survival can compensate for any initial differences in seedling abundance (Harper 1977). Yet, despite the importance of these arguments in shaping thinking about the population impacts of herbivory, we know of no empirical study that has experimentally determined how prevalent these factors are in minimizing the effects of herbivory on plant abundance.

Given the importance of seed- versus safe-site limitation, seedbank longevity, and density-dependent seedling survival to the debate regarding the population-level effects of herbivores, we sought to explore more precisely how these factors might be expected to mediate the influence of consumers on plant abundance. Our simulation results reveal that reductions in seed production due to herbivory can have surprisingly large impacts on plant abundance, even under conditions thought to minimize the population effects of herbivory. For example, given a long-lived seedbank, average population abundance can be significantly affected by herbivory even when recruitment is uncorrelated with seed density in a majority of years or in space (Figs. 4, 5). In fact, this model predicts that herbivory can have as large a relative effect on plant abundance under these circumstances as it can under conditions where the link between seed production and seedling abundance is strong – that is, when there is no seedbank and recruitment is always seed-limited.

We ran the model over a range of parameter values that a priori we thought might constrain the population

response to herbivory. For example, in the model, seedling mortality was high (70%), and density dependence was always strong enough to increase this value to 95% mortality at high seedling density. Despite the compensatory nature of this density dependence, given a long-lived seedbank and seed-limited recruitment in a minimum of 20% of years or cells, the population response to herbivory was still substantial. In model runs with extreme (99%) density-dependent mortality, density dependence could almost always compensate for gains in recruitment due to the absence of herbivory, as one might expect. The point here, however, is not that density-dependent mortality can be compensatory at some upper bound. Instead, the important consideration is that even with a high degree of compensatory mortality, consumers that reduce plant fecundity can have a heretofore unappreciated influence on autotroph abundance.

Results suggest the significance of a long-lived seedbank in shaping the plant population response to herbivory. Previous discussions of the population effects of herbivores have focused on the role of seedbanks in buffering the population impacts of herbivory (Crawley 1992; Louda and Potvin 1995). This buffering capacity is clearly an important function; as an illustration of this, simulated populations subjected to herbivory were consistently much smaller in the absence of a seedbank than when one was present. However, in addition to acting as a buffer, the seedbank acts as a memory that “stores” the cumulative effects of herbivory through time. In simulations, even infrequent pulses of seed-limited recruitment enabled accumulated seed loss from herbivory to be expressed in terms of reduced seedling recruitment and adult abundance. Significant reductions in population size were detected even when averaged across many years where recruitment was safe-site-limited and therefore uncorrelated with seedbank abundance.

How might simulation results with either temporal or spatial variation in seed-limited recruitment relate to what occurs in nature? One can think of temporal variation in seed-limited recruitment as capturing the process of episodic recruitment. Many plants experience pulsed recruitment out of a seedbank, triggered by fire, heavy rainfall or other disturbance events that increase the number of safe-sites (Juhren 1956; Noy-Meir 1973; Christensen 1985; Enright and Lamont 1989). During episodic recruitment, there may be a reasonable correlation between seedbank density and the number of recruits that establish, even given strong density-dependent seedling survival. Even though these periods may be separated by many years with only sporadic germination (and therefore little correspondance between seedling and seedbank density), model output illustrates that episodic seed limitation that occurs in 2 years out of 10 can provide a mechanism by which the negative impacts of herbivory can be felt at the population level. Environmental stimuli that trigger recruitment, such as heavier than normal rainfall or fire, can occur at such intervals (Hall et al. 1964; Savage and Swetnam 1990; Figueroa and Davy 1991).



In contrast to temporal variation in seed-limited recruitment, spatial variation in seed-limited recruitment in the model is meant to simulate small-scale disturbances (such as gopher mounds) that open up sites for germination (Rapp and Rabinowitz 1985; Milton et al. 1997; Edwards and Crawley 1999). On this small spatial scale, these “disturbed” sites produce local hotspots where recruitment is seed-limited. Here again, if 20% of sites are disturbed, herbivores that reduce seed production can have meaningful impacts of plant populations. Given spatial variation in seed-limited recruitment, herbivory can also significantly decrease spatial aggregation; sensitivity analysis revealed that herbivory accounted for 21% of the variance in the coefficient of variation in population abundance. Sensitivity analysis also highlights the importance of stochasticity in demographic rates to population abundance. This suggests that while consumers can be important to plant population dynamics, detecting their effects in a spatially and temporally heterogeneous world may be challenging, and will require large sample sizes and long-term studies.

Taken together, simulation results reveal that the range of conditions under which reductions in plant fecundity can influence long-term population abundance may be broader than previously thought. Empirical tests are now needed to determine whether seed-limited recruitment need only occur a small percentage of time (or in space) for population-level effects of herbivory to be manifest. These empirical studies would ideally include field assays to determine the extent to which recruitment into populations is likely to be seed or safe-site-limited. In theory, this would involve a determination of whether all safe sites were saturated with seeds, since it is only at this point that the population would cease to be seed-limited.

Lacking empirical evidence for the population effects of consumers, debate regarding consumers and plant population dynamics has too often centered around the dichotomy of whether plant populations are seed or safe-site-limited. We suspect that for many plants this dichotomy is false. Plants may experience both seed and safe-site limitation in the same year (Eriksson and Ehrlén 1992) or recruitment may oscillate between being seed-limited in some years and safe-site-limited in others, as the size of seed crops and environmental cues that trigger germination vary. Therefore, the important issue for plants with temporally pulsed or spatially clumped germination is not whether they are seed-limited, but the frequency with which seeds or safe-sites limit germination.

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## References

- Andersen AN (1988) Insect seed predators may cause far greater losses than they appear to. *Oikos* 52:337–340
- Andersen AN (1989a) How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia* 81:310–315
- Andersen AN (1989b) Pre-dispersal seed losses to insects in species of *Leptospermum* (Myrtaceae). *Aust J Ecol* 14:13–18
- Auld TD (1986) Variation in predispersal seed predation in several Australian *Acacia* spp. *Oikos* 47:319–326
- Auld TD, Myerscough PJ (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: seed production and predispersal seed predation. *Aust J Ecol* 11:219–234
- Carson WP, Root RB (2000) Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecol Monogr* 70:73–99
- Christensen NL (1985) Shrubland fire regimes and their evolutionary consequences. In: Pickett STA, White PS (eds) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, pp 85–100
- Crawley MJ (1989a) Insect herbivores and plant population dynamics. *Annu Rev Entomol* 34:531–564
- Crawley MJ (1989b) The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In: Bernays EA (ed) *Insect-plant interactions*. CRC, Boca Raton, pp 45–71
- Crawley MJ (1990) The population dynamics of plants. *Philos Trans R Soc Lond* 330:125–140
- Crawley MJ (1992) Seed predators and plant population dynamics. In: Fenner M (ed) *Seeds, the ecology of regeneration in plant communities*. CAB International, Wallingford, pp 157–192
- Crawley MJ, Pacala SW (1991) Herbivores, plant parasites, and plant diversity. In: Toft CA, Aeschlimann A, Bolis L (eds) *Parasite-host associations: coexistence or conflict?* Oxford Science, Oxford, pp 157–173
- Doak DF, Marino PC, Kareiva PM (1992) Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theor Popul Biol* 41:315–336
- Duggan AE (1985) Predispersal seed predation by *Anthocharis cardamines* (Pieridae) in the population dynamics of the perennial *Cardamine pratensis* (Brass.). *Oikos* 44:99–106
- Edwards GR, Crawley MJ (1999) Herbivores, seedbanks and seedling recruitment in mesic grassland. *J Ecol* 87:423–435
- Enright NJ, Lamont BB (1989) Seedbanks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *J Ecol* 77:1111–1122
- Eriksson O, Ehrlén J (1992) Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91:360–364
- Evans EW, Smith CC, Gendron RP (1989) Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. *Oecologia* 78:220–230
- Figueroa ME, Davy AJ (1991) Response of Mediterranean grassland species to changes in rainfall. *J Ecol* 79:925–941
- Fowler NL (1988) What is a safe site? Neighbor, litter, germination date, and patch effects. *Ecology* 69:947–961
- Green TW, Palmblad IG (1975) Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). *Ecology* 56:1435–1440
- Gross KL (1980) Colonization by *Verbascum thapsus* (mullein) of an old field in Michigan: experiments on the effects of vegetation. *J Ecol* 68:919–927
- Hairston NB Jr, Hairston NG (1993) Cause-effect relationships in energy flow, trophic structure and interspecific interactions. *Am Nat* 142:379–411
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- Hall EA, Specht RL, Eardley CM (1964) Regeneration of the vegetation on Koonamore vegetation reserve 1926–1962. *Aust J Bot* 12:205–264

- Harper JL (1977) Population biology of plants. Academic Press, London
- Hawthorne WR, Cavers PB (1976) Population dynamics of the perennial herbs *Plantago major* L. and *P. rugelii* Decne. *J Ecol* 64:511–527
- Hendrix SD (1979) Compensatory reproduction in a biennial herb following defoliation. *Oecologia* 42:107–118
- Hendrix SD (1984) Reactions of *Heracleum lanatum* to floral herbivory by *Depressaria pastinacella*. *Ecology* 65:191–197
- Hunter MD (1992) Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. In: Hunter MD, Ohgushi T, Price PW (eds) Effects of resource distribution on animal-plant interactions. Academic Press, New York, pp 288–325
- Jermy T (1984) Evolution of insect/host plant relationships. *Am Nat* 124:609–630
- Jermy T (1993) Evolution of insect-plant relationships – a devil's advocate approach. *Entomol Exp Appl* 66:3–12
- Juhren M, Went FW, Phillips E (1956) Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology* 37:318–330
- Louda SM (1982a) Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. *J Ecol* 70:43–53
- Louda SM (1982b) Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecol Monogr* 52:25–41
- Louda SM (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology* 64:511–521
- Louda SM (1989) Predation in the dynamics of seed regeneration. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seedbanks. Academic Press, New York, pp 25–51
- Louda SM (1995) Experimental evidence for insect impact on populations of short-lived, perennial plants, and its application in restoration ecology. In: Bowles ML, Shelan CJ (eds) Restoration of endangered species. Cambridge University Press, Cambridge, pp 118–138
- Louda SM, Potvin MA (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76:229–245
- Maron JL (1998) Insect herbivory above- and below-ground: individual and joint effects on plant fitness. *Ecology* 79:1281–1293
- Milton SF, Dean WRJ, Klotz S (1997) Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. *J Veg Sci* 8:45–54
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–51
- Pearl DR (1989) Species interactions in a successional grassland. I. Seed rain and seedling recruitment. *J Ecol* 77:236–251
- Putwain PD, Machin D, Harper JL (1968) Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella* L. *J Ecol* 56:421–431
- Rapp JK, Rabinowitz D (1985) Colonization and establishment of Missouri Prairie plants on artificial soil disturbances. I. Dynamics of forb and graminoid seedlings and shoots. *Am J Bot* 72:1618–1628
- Rees M, Paynter Q (1997) Biological control of Scotch broom: modeling the determinants of abundance and the potential impact of introduced insect herbivores. *J Appl Ecol* 34:1203–1211
- Root RB (1996) Herbivore pressure on goldenrods (*Solidago altissima*) – its variation and cumulative effects. *Ecology* 77:1074–1087
- Sagar GR, Harper JL (1960) Factors affecting the germination and early establishment of plantains (*Plantago lanceolata*, *P. media* and *P. major*). In: Harper JL (ed) The biology of weeds. Blackwell, Oxford, pp 236–245
- Savage M, Swetnam TW (1990) Early nineteenth-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71:2374–2378
- Shaw RG, Antonovics J (1986) Density dependence in *Salvia lyrata*, a herbaceous perennial: the effects of experimental alteration of seed densities. *J Ecol* 74:797–813
- Sheppard AW (1987) Insect herbivore competition and the population dynamics of *Heracleum sphondylium*, L. (Umbelliferae). PhD thesis, University of London
- Symonides E (1979) The structure and population dynamics of psammophytes on inland dunes: populations of initial stages. *Ekol Pol* 27:3–37
- Waloff B, Richards RO (1977) The effect of insect fauna on growth mortality and natality of broom, *Sarothamnus scoparius*. *J Appl Ecol* 14:787–789
- Wise MJ, Sacchi CF (1996) Impact of two specialist insect herbivores on reproduction of horse nettle, *Solanum carolinense*. *Oecologia* 108:328–337
- Zammit C, Hood CW (1986) Impact of flower and seed predators on seed-set in two *Banksia* shrubs. *Aust J Ecol* 11:187–193