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SPATIAL PATTERNING IN PLANTS: OPPOSING EFFECTS OF HERBIVORY AND COMPETITION

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SUMMARY

(1) A field experiment was conducted to determine how the spatial distribution of *Poa annua* influenced the ability of *Senecio vulgaris* to establish in experimental plots. The relative effects of slug herbivores, dead individuals of *Poa annua* and live individuals of *Poa annua* on *Senecio* establishment were also investigated.

(2) *Senecio* exhibited a higher rate of population growth when planted amidst clumped *Poa* than when planted amidst a random distribution of *Poa*. This change in population growth is due to increased survival of *Senecio* seedlings which emerge in areas having a low density of dead *Poa*.

(3) The advantage associated with a clumped distribution of *Poa* was opposed by two other consequences of spatial distribution: herbivores consumed more *Senecio* seedlings, and intraspecific competition among *Senecio* seedlings was greater, where the grass was clumped than where it was randomly distributed.

(4) Despite a number of direct effects, higher-order interactions and indirect effects, the net result of spatial patchiness is easily understood in this system because seedling suppression by dead *Poa* has overriding importance.

INTRODUCTION

Because plants are sessile, it is inappropriate to think of interactions among them as occurring within a homogeneous group of individuals. As a consequence, some plant ecologists (e.g. Marshall & Jain 1969; Law 1981; Weiner & Conte 1981; Grubb 1986; Hutchings 1986) have suggested that it may be difficult to understand plant population dynamics in the field. The difficulty arises because an apt description of plant populations apparently requires detailed knowledge about the spatial arrangement of plants and how that spatial arrangement influences species interactions.

Although many researchers have recently begun to examine spatial dispersion as a factor in plant dynamics, these efforts have focused on simplified aspects of species dispersion. Theoreticians have demonstrated that aggregation may eliminate competitive exclusion (Atkinson & Shorrocks 1981; Weiner & Conte 1981; Ives & May 1985; Pacala 1986a,b; Pacala & Silander 1990), but they neglect its effect on factors that might also influence competing species. In contrast, empiricists have explored the consequences of plant patchiness for each of several traits: adult fecundity (e.g. Ross & Harper 1972; Mithen, Harper & Weiner 1984; Silander & Pacala 1985), seedling establishment (e.g. Gross 1980; Goldberg & Werner 1983), pollinator flight patterns (reviewed in Handel 1983), and the distribution of herbivores (reviewed in Kareiva 1983). Although these empirical studies suggest that spatial pattern can influence between-generation dynamics in a number of ways, they are limited in that only short-term effects are investigated and each consequence of spatial pattern has been studied in isolation.

Previous experiments have revealed that, when it competes with *Poa annua*, *Senecio vulgaris* is more successful when *Poa* is clumped rather than randomly distributed

(Bergelson 1990). These experiments suggested that the dispersion of dead grass influenced *Senecio* success as a result of between-generation competitive effects on seedling survival, but these competitive effects were insufficient to explain the abundance and distribution of invading *Senecio* seedlings. The goal of the present experiment is to explore the influence of plant spacing in the context of a rich variety of inter- and intraspecific interactions including herbivory, within-generation competition and between-generation competition. This study builds on past work by (i) directly testing the role of dead *Poa* in determining the observed patterns of *Senecio* seedling abundance, (ii) by examining the effects of herbivory, which may interact with the spatial distribution of dead *Poa* in determining patterns of *Senecio* seedling abundance, (iii) quantifying how patterns of *Senecio* seedling abundance influence the numbers and distribution of adults, and (iv) investigating 'indirect effects' on intraspecific competition in *Senecio* caused by dead *Poa* and herbivores. 'Indirect effects' would result if herbivory or dead *Poa*, or both, cause non-random mortality which alters the spatial pattern of *Senecio* seedlings, and thereby mediates the intensity of intraspecific competition.

MATERIALS AND METHODS

Species

Senecio vulgaris L. (groundsel) is a small composite that typically completes two generations per year in Seattle, Washington, USA. *Senecio* has several advantages for a study on competition: it produces many inflorescences which are self-fertile; seeds have only limited dormancy (Roberts 1964; Roberts & Feast 1973); reasonably accurate estimates of fecundity (i.e. seed number) can be obtained simply by counting the number of flower heads produced (Bergelson 1990); and populations develop rapidly and synchronously in both spring and autumn (personal observations).

Senecio was subjected to competition with background populations of *Poa annua* L. (annual bluegrass). These species commonly co-occur throughout the United States. Like *Senecio*, *Poa* is self-fertile and has seeds with limited dormancy. *Poa* develops more slowly than *Senecio*, although it also completes a spring and autumn generation each year. Because it is very difficult to distinguish genetic individuals of grass under sward conditions, I ignore the population dynamics of *Poa* and instead use it as a treatment factor to be manipulated in these experiments.

Experiments

The experiment described in this study spanned two generations. *Poa* seeds were sown in each of two spatial patterns and *Senecio* seeds were sown randomly. All individuals were left undisturbed (in the absence of slugs) until the seeds of *Senecio* had dispersed. Two additional treatments were then established: the presence or absence of slugs (*Agriolimax reticulatus* Muller and *Limax maximus* L.) and the presence or absence of dead *Poa* from the spring (preceding) generation. Because the appropriate scale of measurement was unknown (e.g. at what scale herbivores are sensitive to seedling aggregations, or at what scale the fecundity of adults is sensitive to the density of competitors), observations were recorded on two spatial scales as outlined below.

Plots

On 14 May 1988, twenty-four 1-m × 1-m plots were dug to a depth of 20 cm and filled with a mixture of steam-sterilized soil and 14–14–14 NPK fertilizer at a concentration of

350 g m^{-2}. These plots were randomly assigned to each of two groups. In one group *Poa* was sown in a clumped spatial pattern (negative binomial distribution, $K=1$, mean $= 14\cdot4$) and in the other *Poa* was sown randomly (Poisson distribution, mean $= 14\cdot4$). *Senecio* was always sown randomly. Although a somewhat objective index of dispersion, these patterns correspond to approximately 25% and 15% bare ground, respectively, once the grass was full-grown. Patterns were obtained by dividing each plot into twenty-five 20-cm × 20-cm squares and randomly assigning seedling densities to each square by a unique draw from the appropriate distribution. Squares were overseeded and seedlings were thinned to the appropriate density within three days of emergence. There were ninety *Senecio* and 360 *Poa* seedlings in each plot.

Senecio began flowering in early August. On 11 August, ten *Senecio* individuals from each plot were sampled. A nested analysis of variance confirmed that there was no difference in the fecundity of surviving *Senecio* subjected to the two treatments ($F_{1,23} = 0\cdot20$, $P > 0\cdot65$). These results agreed with more extensive sampling performed under identical conditions in the previous year. Because equal numbers of *Senecio* survived to flower in the random and patchy plots ($F_{1,23} = 0\cdot09$, $P > 0\cdot35$), these fecundity results indicate that an equivalent number of seeds had been introduced into the two plot types at the beginning of the autumn (second) generation. Two new treatments (removal of dead grass: CUT vs. NOT CUT; exclusion of slugs: SLUGS vs. NO SLUGS) were superimposed on each plot on 31 August. By this time, *Senecio* plants had finished dispersing their seeds although seedlings had not yet emerged. Essentially all *Senecio* and *Poa* individuals from the spring generation died and dried up during August. Morphological differences between the species meant that dead *Senecio* blew away during August while dead *Poa* remained intact throughout the autumn (second) generation.

This sequence of manipulations established a three-way factorial experiment, in which the factors were (i) the distribution of *Poa* in the previous generation (random vs. clumped), (ii) the presence or absence of slugs, and (iii) the presence or absence of above-ground biomass from dead *Poa*. There were three replicates of each treatment combination. Plots were kept free of non-experimental plants by weekly weeding, and all plots were watered on alternate days. In the CUT treatment grass from the previous generation was cut weekly at ground level and in the NO SLUG treatment a proprietary slug and snail poison was applied on alternate weeks. The number of slugs grazing in each plot was counted eight times throughout the season.

Plots were censused three times during the autumn (second) generation: on 20 September to determine *Senecio* seedling numbers; on 3 November to determine the number of *Senecio* adults; and on 30 November to determine the estimated fecundity (number of flower heads) of these adults. Because all plots begin with the same number of *Senecio* seedlings in the first generation, these measures of *Senecio* abundance in the second generation correspond to measures of relative growth rate.

Quadrats

On 12 September, after many seedlings had emerged in the plots, the simple size structure of the population made it possible to investigate the early fate of seedlings (which emerge too densely to mark individually). A quadrat that had been divided into twenty-five 4-cm × 4-cm squares was superimposed on four randomly chosen 20-cm × 20-cm squares plot^{-1} and the number of seedlings in each of the 4-cm × 4-cm squares was recorded. Two weeks later, these individuals had developed true leaves. Individuals in the 4-cm × 4-cm squares were recounted in order to determine how slugs and the presence of

dead *Poa* had altered the number and position of surviving seedlings. The four replicate quadrats were resampled in only sixteen of the original twenty-four plots; these quadrats were selected to represent two replicates of each treatment combination. Note that quadrats represent a subsample of the 20-cm × 20-cm squares, and refer to squares that were subdivided for investigating interactions on a smaller spatial scale.

Statistical analysis

Data on (i) the number of *Senecio* seedlings plot^{-1} (ii) the number of adults plot^{-1} and (iii) the estimated fecundity of adults, were analysed by applying three-way analyses of variance to the mean values for each plot. The factors in these analyses were: the effects of slugs, the spatial pattern of dead *Poa*, the removal of dead *Poa*, and all higher-order interactions. In addition, data on the number of seedlings within the quadrats through time (between 12 September and 26 September) were used to determine the effect of slugs and dead *Poa* on the early survival of *Senecio* seedlings. Effects of spatial distribution were not investigated because that treatment was applied on a scale larger than the 400-cm^2 quadrats.

In order to determine how the spatial pattern of *Senecio* changes with time, measures of dispersion on the scale both of the (1-m × 1-m) plot and the 400-cm^2 quadrat were calculated. On the scale of the plot, the coefficients of variation (CV) for seedlings and for adults derived from these seedlings were calculated, where the CV refers to the standard deviation in abundance among the twenty-five 20-cm × 20-cm squares within each full plot divided by the mean abundance in these squares. The proportional change in the CV, defined as (CV seedlings − CV adults)/CV seedlings, was used as a measure of the change in the spatial distribution. An analysis of variance was performed on this statistic (which was distributed normally and had homogeneous variances), using spatial distribution, dead grass, and slugs as the experimental factors and including all higher-order interactions. On the scale of the quadrat, the effects of slug herbivory and dead grass on spatial distribution were similarly analysed by comparing the proportional changes through time (from cotelydon to first leaf) in the CV of the seedling distribution within the twenty-five 4-cm × 4-cm squares.

Finally, in order to determine how the spatial distribution of *Senecio* influences intraspecific competition, indices of dispersion were again calculated. On the scale of the plots, CV was used as an index of seedling dispersion. (There was no significant correlation between this index and density; Spearman rank correlation $= 0.57$, $n = 12$, $P > 0.05$.) On the smaller scale of the quadrat, CV/n was used as an index of dispersion because it was not correlated to density (correlation coefficient $= 0.1949$, $n = 32$, $P > 1.10$), whereas there was a correlation between density and CV itself (correlation coefficient $= 0.4356$, $n = 32$, $P < 0.02$).

RESULTS

Direct effects and higher-order interactions

Plots

Both the presence of slugs and of dead grass reduced the abundance of *Senecio* seedlings (Table 1). When dead grass was present, significantly more seedlings grew amidst a patchy distribution of *Poa*. The significant interaction between *Poa* distribution and slug presence occurred because the inhibitory effect of slugs was greatest within a patchy distribution (Fig. 1a,b). Adult numbers were generally less affected by the

Table 1. Plot-level analysis of variance on the performance of Senecio vulgaris ($F_{1,16}$ values). SLUGS indicates the presence or absence of Agriolimax reticulatus and Limax maximus in the plots, DIST refers to the spatial distribution of Poa annua (either random or patchy) and CUT indicates whether or not dead Poa annua was removed before seedlings of the second generation emerged.

	Main effects		
Dependent variables	SLUGS	DIST	CUT
Number of Senecio seedlings	14·31***	10·02***	18·33***
Number of Senecio adults	0·03	45·45***	0·81
Fecundity	1·53	0·53	0·01

	Interactive effects			
Dependent variables	CUT × SLUG	CUT × DIST	DIST × SLUG	DIST × CUT × SLUG
Number of Senecio seedlings	0·42	4·65*	6·97*	1·94
Number of Senecio adults	39·60**	4·27	0·98	61·16***
Fecundity	3·06	0·03	0·25	0·00

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

experimental treatments than were seedlings. In particular, significantly more adults were found amidst patchily distributed grass, yet neither dead grass nor slugs affected adult numbers (Fig. 1c,d). Lastly, the estimated fecundity of adults was not different with respect to any of the experimental factors (Fig. 1e,f).

Quadrats

A significantly higher mortality was associated with the presence of slugs ($F_{1,59} = 39.927$, $P<0.001$) and the presence of dead grass ($F_{1,59} = 32.804$, $P<0.001$), but the interaction between these two factors was not significant ($F_{1,59} = 0.081$, $P>0.75$).

Because the fate of individuals in each quadrat was followed, it was possible to assess how early seedling numbers influenced their survivorship and subsequent fecundity for this subset of the larger plots. The probability of a seedling surviving to adulthood was a decreasing non-linear function of the number of conspecific seedlings (Fig. 2a), although no relationship existed between the number of initial seedlings and the fecundity of surviving adults (Fig. 2b).

Plots with dead grass

A census of slug abundances revealed that these herbivores abandoned plots in which the above-ground biomass of Poa was removed. When dead Poa was present, similar numbers of slugs (mean ± 2 S.E.) were found in the patchy and random plots (3.88 ± 0.15 and 4.17 ± 0.16 plot^{-1}, respectively) but slugs were never found in the plots without dead grass. This observation indicated that it was most appropriate to investigate slug effects in the presence of dead grass.

When only the twelve plots with dead Poa are considered (Table 2), seedling numbers are still reduced by a random distribution of dead Poa and the presence of herbivores, and these two factors still have a significant interaction. Adult distributions reflect the distribution of seedlings. There are fewer adults in the presence of slugs or a random distribution of dead grass, and slugs have a greater impact when dead Poa is distributed patchily. Finally, neither dead Poa nor slugs had an effect on the average fecundity of adults.

To understand the cause of this interaction better, the amount of seedling herbivory in 20-cm × 20-cm squares corresponding to a range of seedling numbers was estimated. The
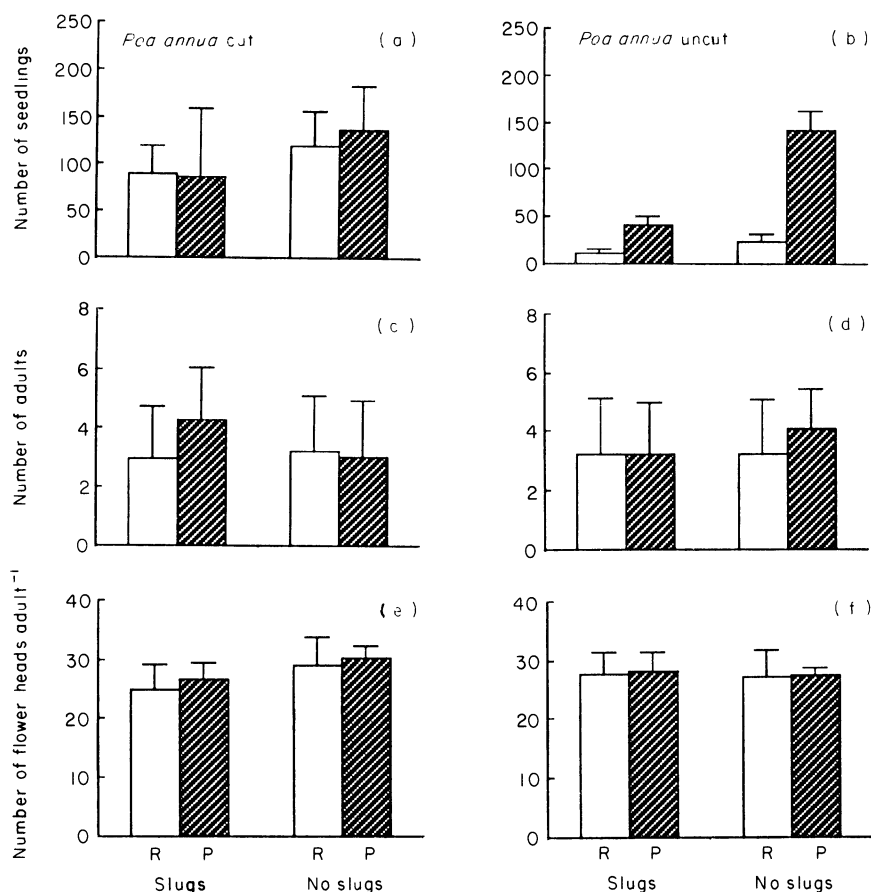
FIG. 1. (a, b) Number of seedlings of *Senecio vulgaris* in the autumn generation; (c, d) number of adults in the autumn generation; (e, f) production of flower heads by adults in the autumn generation in treatments with the *Poa annua* cut (a, c, e) and uncut (b, d, f). R = random distribution and P = patchy distribution of *Poa*. Mean ± 2 S.E. are shown for each of the eight plot types.

index of herbivory used was the difference between the average number of seedlings found when slugs were absent and when slugs were present for squares with the same densities of dead *Poa*. Squares were matched in this way because the amount of dead *Poa* in this area is a good predictor of the number of *Senecio* seedlings expected there (Bergelson 1990).

Most of the herbivory occurred in areas where seedling densities are high (Fig. 3). When all the data are considered together, a positive association between seedling numbers and slug herbivory is detected ($F_{1,37} = 5.54$, $P < 0.05$). Closer observation reveals some subtleties. There was a significant positive correlation between the estimated intensity of herbivory and the number of *Senecio* seedlings within a square in the patchy plots (Spearman rank correlation coefficient = 0.48, $n = 22$, $P < 0.05$) but no such correlation in the random plots (Spearman rank correlation coefficient = 0.21, $n = 17$, $P > 0.10$). While the unequal variances in mortality experienced by seedlings in the patchy and random plots precludes statistical verification that slug herbivory is distributed differently within the two plot types, it appears that slugs aggregate their feeding in dense pockets of *Senecio*
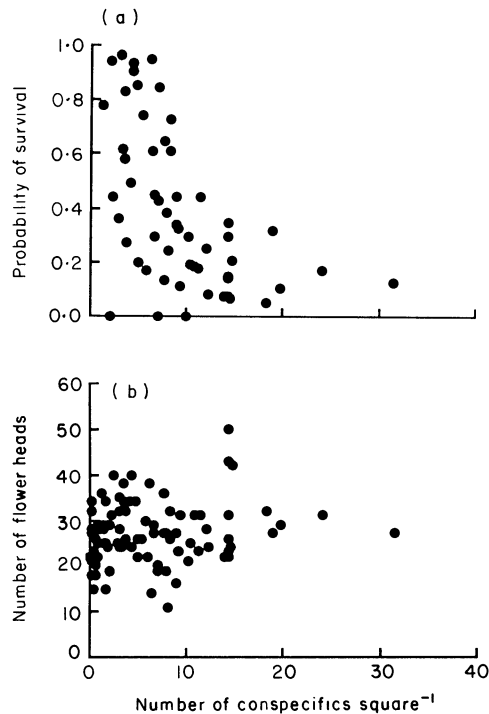
FIG. 2. The performance of individuals of *Senecio vulgaris* found in the 20-cm × 20-cm squares. (a) Survival of *Senecio* seedlings to adult plants as a function of the number of conspecific seedlings. (b) The fecundity of those seedlings that survive to adult plants as a function of the number of conspecifics.

seedlings (which are found in areas having a low density of dead *Poa*; Bergelson 1990) when *Poa* is patchily but not randomly distributed. Because many more of these *Senecio* aggregates occur amidst a patchy distribution of *Poa*, slug consumption is higher in these patchy plots.

Indirect effects of herbivores and dead grass

In addition to the direct effects described above, herbivores and dead *Poa* may influence competition by altering the spatial pattern of *Senecio* seedlings, thereby augmenting or reducing the intensity of intraspecific competition.

TABLE 2. Two-way analysis of variance of the performance of *Senecio vulgaris* in the presence of dead *Poa annua* (F values).

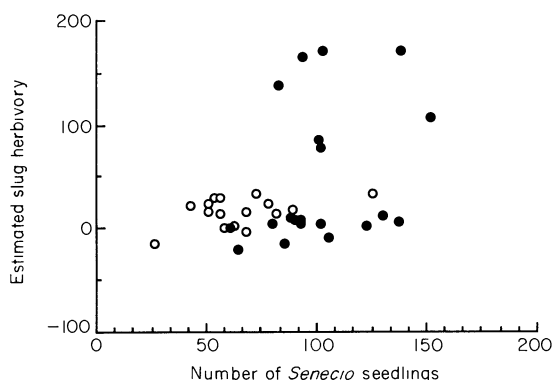|		Effects	
Dependent variable	DIST	SLUGS	DIST × SLUGS
Number of *Senecio* seedlings	132·51***	77·21***	49·52***
Number of *Senecio* adults	26·09***	29·45***	26·09***
Fecundity	0·03	0·14	0·01

***$P < 0.001$.

Herbivory vs. competition

FIG. 3. Estimated amount of slug herbivory as a function of the number of *Senecio vulgaris* seedlings occupying a 20-cm × 20-cm square in the full plots. Slug herbivory was measured as the average difference in the number of *Senecio* seedlings found when slugs were absent and when slugs were present for squares with the same densities of dead *Poa*. Plants within plots have either randomly (O) or patchily (●) distributed grass.

Changes in Senecio *spatial distribution*

An analysis of variance on the proportional change in the spatial distribution of seedlings within the full plots indicated that slugs ($F_{1,23} = 7.04$, $P < 0.02$), dead *Poa* ($F_{1,23} = 13.83$, $P < 0.002$) and a random distribution of dead *Poa* ($F_{1,23} = 19.60$, $P < 0.0004$) tend to randomize the spatial distribution of *Senecio* seedlings. An analysis of variance on the scale of the 400-cm² quadrats demonstrated that the change in CV was significantly greater in the presence of slugs than in their absence ($F_{1,62} = 22.29$, $P < 0.0001$). Again, herbivory tended to make the spatial pattern less aggregated, just as was observed at the larger scale. There was no significant effect of dead *Poa* ($F_{1,62} = 0.10$, $P > 0.75$), and no significant interactions.

Influence of spatial distribution on intraspecific competition

The effect of this decreased patchiness on intraspecific competition was investigated in the twelve cut plots. The removal of dead grass causes slugs to abandon the plot. Consequently, seedlings in these plots are not subject to mortality due either to dead plants or to herbivores.

There was a significant decrease in the probability of survival (arcsin square-root transformed; $F_{1,11} = 2.72$, $P < 0.025$; Fig. 4a) with an increase in patchiness (as measured by the CV) on the scale of the full plot. The significance of this relationship is unaffected by omitting the outlying point. As a result of this mortality, there were fewer plants present as adults ($F_{1,11} = 8.471$, $P < 0.02$) in a patchy environment (Fig. 4b); the surviving adults, however, enjoyed an increased production of flower heads ($F_{1,11} = 2.42$, $P < 0.04$) (Fig. 4c). There were no significant effects of dispersion within a quadrat (as measured by CV/n) on the fecundity ($F_{1,28} = 1.02$, $P > 0.3$) or the (arcsin square-root transformed) percentage survival ($F_{1,28} = 0.47$, $P > 0.6$) of individuals. These results would not have changed had CV been used as an index of dispersion instead.

DISCUSSION

These experiments show that the specific arrangement of *Poa annua* influences the interactions of its competitor in a variety of ways. The primary effect of an aggregated
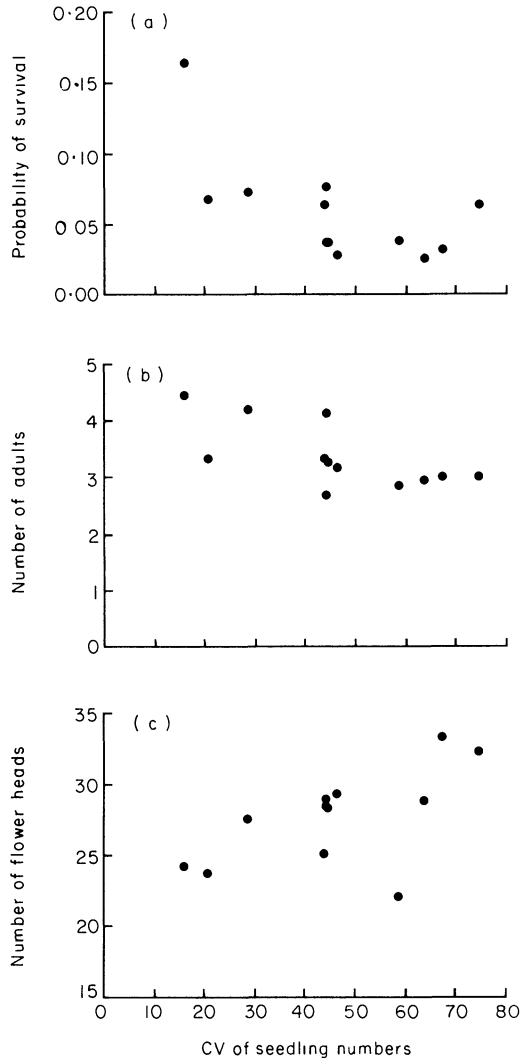
Fig. 4. The performance of seedlings of *Senecio vulgaris* in the 1-m × 1-m full plots without herbivores or litter as a function of the spatial dispersion of seedlings (measured by the coefficient of variation (CV) in the abundance of seedlings in each of the twenty-five 20-cm × 20-cm squares in each plot). (a) The survival of *Senecio* seedlings. (b) The number of adults. (c) The fecundity of surviving adults.

distribution of dead *Poa* is to provide areas of low density that enable seedlings to establish. Results from previous work (Bergelson 1990) suggest that these areas are necessary for the establishment of *Senecio* seedlings because dead grass severely increases seedling mortality. In the present experiments, dead *Poa* was generally dense enough to inhibit the establishment of seedlings. While there is heterogeneity in the density of dead *Poa* when it is distributed either randomly or patchily, there is greater variance in the density of dead *Poa* as patchiness increases. This necessarily means that there are more areas with low densities when *Poa* is patchily distributed, and it is these areas that

facilitate seedling establishment. It is important to note that seedling establishment is not restricted to gaps having no dead grass. Patchiness increases the proportion of areas having low densities, and these areas provide a continuum of sites that may prove suitable for establishment. In essence, it is the change in the proportion of areas with a low density of dead *Poa* that mediates the effect of spatial pattern in these experiments. Likewise, it is this change that drives the benefits associated with patchy distributions in mathematical models (e.g. Atkinson & Shorrocks 1981; Hanski 1981; Ives & May 1985; Pacala 1986a,b).

Opposing this benefit in terms of seedling establishment are two detrimental effects of a patchy distribution of dead *Poa*. The first of these is evident in the interaction between slug herbivory and the distribution of dead *Poa*. Slugs inflicted greater mortality to seedlings amidst a clumped as opposed to a random distribution of *Poa*. The observed behaviour of slugs was exactly the pattern that would be predicted from the resource-concentration hypothesis (Root 1973). A clumped distribution of dead *Poa* opens gaps, enabling high rates of establishment by *Senecio* seedlings; the resultant aggregations of *Senecio* seedlings are subject to intense slug herbivory (see Fig. 3). This means that slug herbivory tends to counteract the advantage that seedlings acquire by avoiding dead *Poa* in gaps.

In addition, the improved success of *Senecio* seedlings amidst an aggregated distribution of dead *Poa* is further offset by increased intraspecific competition among *Senecio* seedlings that are aggregated in areas with little dead *Poa*. This competitive effect results in lower seedling survivial, which is expected when dense aggregations of seedlings can lead to only few adults. Paradoxically, the increased intraspecific competition associated with aggregation led also to an *increase* in the fecundity of survivors; this pattern probably results from a reduction in the number of adults caused by increased competition.

While seedling numbers are reduced in the presence of both slugs and dead grass, only slug herbivory persists to influence adult numbers. Herbivory is generally accepted to be important in determining seedling success (Crawley 1983), and slugs are known to be particularly voracious seedling predators (e.g. Dirzo & Harper 1980). Litter, too, is often found to inhibit the germination or emergence of seeds (King 1975; Gorski, Gorski & Nowicki 1977; Silvertown 1980) and the survival of seedlings (Sydes & Grime 1981; de Jong & Klinkhamer 1985). Lack of an effect of dead *Poa* on adult numbers suggests that dead grass causes mortality levels similar to the self-thinning which occurs among *Senecio* seedlings in the absence of dead grass.

These experimental results illustrate two additional points. First, the scale of measurement may influence the interactions which are uncovered. Whereas the effects of slug herbivores and dead grass are insensitive to the scale of measurement, statistical effects associated with intraspecific competition are not consistent across spatial scales. For instance, a high density of conspecifics reduced survival only at the small scale and plant dispersion influenced survival only on the large scale. I interpret these results to mean that differences in the local density of competitors lead to differences in the performance of individuals (for further examples, see Mack & Harper 1977; Silander & Pacala 1985; Pacala & Silander 1987), whereas it is the spatial pattern on a larger scale that causes these local density patterns. Secondly, these experimental results suggest that herbivory and between-generation competitive effects may have evolutionary consequences. An analysis on the coefficient of variation in the production of flower heads revealed that the absence of slugs and dead *Poa* (i.e. in the cut plots) was associated with a significantly larger coefficient of variation than the presence of slugs and dead grass. This

result suggests that the fitness hierarchy (Waller 1985; Weiner & Thomas 1986; Geber 1989) that develops between *Senecio* individuals can be reduced by the presence of slugs and dead grass.

In summary, the performance of *Senecio* is influenced by spatial distribution through subtle and opposing effects. Although an intricate sequence of events underlies the effect of spatial pattern, its overall impact is easily understood. Seedling suppression by dead grass essentially mediates the effect of spatial pattern on its own. In addition, none of the results is surprising in its own right. For example, the behaviour of slugs is exactly as would be predicted from the resource-concentration hypothesis and trade-offs between different mortality factors have commonly been observed. It is unfortunate that there is no theory capable of synthesizing this web of interactions. These results suggest, however, that complex interactions may be dominated by a few simple effects.

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