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EXPERIMENTAL STUDIES ON SLUG–PLANT INTERACTIONS

II. THE EFFECT OF GRAZING BY SLUGS ON HIGH DENSITY MONOCULTURES OF *CAPELLA BURSA-PASTORIS* AND *POA ANNUA*

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SUMMARY

(1) Monocultures of *Capsella bursa-pastoris* and *Poa annua* were sown at high density and grown in the presence and absence of the slug *Agriolimax caruanae*. The slug showed strong dietary preference for *Capsella* just as it had done in laboratory tests, and ate *Poa* only after starving for c. 66 h.

(2) The populations of *Capsella* exhibited linear survivorship curves, individuals being lost from the populations at an approximately constant rate.

(3) The rate of self-thinning and the growth made by survivors were such that populations conformed to the $-3/2$ power thinning law, though stands of the two species had different carrying capacity.

(4) Slugs behaved quite differently towards the two plant species. They ate whole, or parts of, leaves of *Capsella bursa-pastoris* but rarely, if ever, killed the plants. They ate *Poa annua* (after the starving threshold) by chewing through shoots at ground level, 'felling' but not consuming the shoots. Many of the damaged plants of *Poa* died.

(5) The effect of slugs was therefore generally to change the size of plants of *Capsella* but not their number and to change the number of plants of *Poa* rather than their size, at least in the early stages of the study.

(6) There was some evidence that defoliation decreased the reproductive potential of the grazed monocultures.

(7) The results are discussed in the context of the compensatory effects of competition and predation, the differential effect of herbivores on plants with different biology, and caveats for other work where grazing trials are involved.

INTRODUCTION

The presence and persistence of a plant population in an area imply that it and its ancestors have survived the recurrent physical hazards typical of that area and these hazards may no longer be the dominant forces directing selection. However the role of biotic forces in natural selection is such that no equilibrium may ever be reached: each evolutionary change in one organism affects the selective forces operating on its competitors, predators or prey, with the consequence that ever-continuing evolutionary processes are maintained and no equilibrium is reached (Levins 1968; Harper 1977).

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Two biotic hazards of prime importance for a plant are (i) the presence of neighbours making demands on the same or similar resources, and (ii) at a different trophic level, the activities of herbivores (or pathogens or both). In many situations neighbours and herbivores probably both act and interact.

The effects of herbivores on their plant prey can vary depending on the kind and amount of plant material removed by the predator, as well as the age or physiological status (or both) of the plant that is damaged (Harper 1977, p. 386). The harm done to the plant will rarely, if ever, be simply measured by the amount of tissue removed. A unit weight removed may, if the plant is a seedling, mean inevitable death, whereas the same unit weight removed from an adult plant may be an almost insignificant fraction of a senile leaf. Moreover, the after-effects of the removal of some plant parts by a predator will depend on the extent to which neighbouring plants are already interfering with each other's activities, because partial defoliation may increase the disadvantage that a plant experiences in the presence of a non-defoliated and competing neighbour.

High density in a plant population causes death or plastic responses or both amongst its members (Harper & Gajic 1961); the response follows a formal mathematical relationship, the $-3/2$ power law (Yoda *et al.* 1963) which is described by $W = Cp^{-3/2}$ (where W is individual plant weight, p is the density of surviving individuals and C a constant). The wide generality of this rule was established by White (1979) and Gorham (1979). Plant populations in which competition is occurring develop a hierarchical structure of suppressed, intermediate and dominant individuals (Obeid, Machin & Harper 1967; Oden 1970; White & Harper 1970; Bazzaz & Harper 1976). The effect of predators on vegetation may therefore need to be seen in the context of the position of the grazed plants in an established hierarchy of a naturally self-thinning population.

The experiments described in this paper were designed to study the influence of a herbivore on plant populations which were dense enough for individual plants to interfere with each other's growth and survival.

MATERIALS AND METHODS

The species

A previous study of the acceptability of a range of plant species to the slug *Agriolimax caruanae* Pollonera (Dirzo 1977) showed that of the two common weedy annuals **Capsella bursa-pastoris* (L.) Medic. and **Poa annua* L., *Capsella* was consistently preferred, whether compared as leaf discs or as intact seedlings. Leaves of *Capsella* were preferred to roots and stems. In the absence of any alternative food, slugs would feed on *Poa* only after a 'starving threshold' of c. 66 h.

In nature, *Agriolimax caruanae* has an annual life cycle with overlapping generations. It is abundant in open and semi-open habitats, commonly in early phases of colonization, e.g. arable lands and gardens but particularly in waste areas. It is absent or very rare in plant communities dominated by grasses. Further details are given in Dirzo (1980). *Agriolimax caruanae* is commonly found in areas where *Capsella* and *Poa* are abundant. Plants of these two species can be found vegetative and often flowering in all seasons and are a *potential* food resource for the slugs throughout the year.

Experiments

Seeds of the two plant species were obtained from commercial suppliers. Seed of *Capsella* requires chilling for a month at 4°C to give satisfactory (55%) germination (Popay

* Referred to hereafter by the generic name alone.

& Roberts 1970). Seed of *Poa* germinated readily (85%) without pre-treatment. One-month-chilled seeds of *Capsella* and non-chilled seeds of *Poa* were used to produce the experimental populations.

Plastic trays (21 × 16 × 5 cm) were filled to within 1.5 cm of the top with John Innes No. 1 Compost. A further layer of finely sifted compost was applied to give a smooth soil surface and seeds were scattered at random. The number of seeds was calculated to give 400 seedlings per tray (12 085 m⁻²). After sowing, the trays were placed in growth cabinets set at 24 °C during the day, 18 °C during the night, with 9 h light per day. Germination was complete after 7 days and the trays were then transferred to a cool glasshouse for 3 days for acclimatization. Seeds of *Capsella* gave a slightly higher germination than expected and the seedling populations were thinned by hand to 420 per tray. Seeds of *Poa* gave populations of seedlings close to the expected density but these were contaminated with other grass species which were removed leaving a realized density of 376 seedlings of *Poa* per tray.

The experimental design involved two treatments (slugs and no-slugs, = grazed and ungrazed) × 2 species of plant × 5 harvests × 2 replicates in a completely randomized design. The five harvests (H1–H5) were taken 9, 17, 25, 39 and 53 days after seedling emergence (10 July 1977). At each harvest the plants were cut at soil level and the above-ground parts were oven-dried and weighed.

Slugs were introduced 4 days after seedling emergence (14 July 1977). A density of two slugs per tray was chosen, based on evidence from previous studies (Hatto & Harper 1969; Harper 1977). Slugs are nocturnal feeders and they were introduced to the plant populations every evening (around 18.00 hours) and removed the following morning (around 9.00 hours). To prevent their escape a removable, completely sealed fence of plastic mesh was fitted to the trays every evening when the slugs were introduced and removed when the slugs were removed in the morning. The slugs were not fed during the day, and an individual slug was always put in the same tray throughout the study.

RESULTS

Ungrazed populations

Biomass production

In the ungrazed trays (Fig. 1), *Capsella* achieved a higher dry weight per plant and per unit area than did *Poa* until H3, but thereafter the yield of *Poa* (per plant and per unit area) became much higher than that of *Capsella*, and continued to increase until the end of the study. *Capsella* is a plant of determinate growth; the first flowering stages were visible after H3 and at that time the rate of dry matter production declined. *Poa*, on the other hand, is a plant of indeterminate growth, and no flowering tillers appeared until the end of the study (H5) at which time vegetative growth and tillering were still active.

Measures of the dry weight of plants per unit area give an incomplete picture of the growth of the population since yield is a function of (i) survivorship and (ii) the distribution of plant weight amongst the survivors.

Survivorship

The trends of survivorship with time (expressed on a logarithmic scale in Fig. 2) show that populations of both species were declining continuously during the course of the experiment. The shapes of the survivorship curves differ in interesting ways. The ungrazed populations of *Capsella* suffered an essentially exponential rate of decay (i.e. individuals

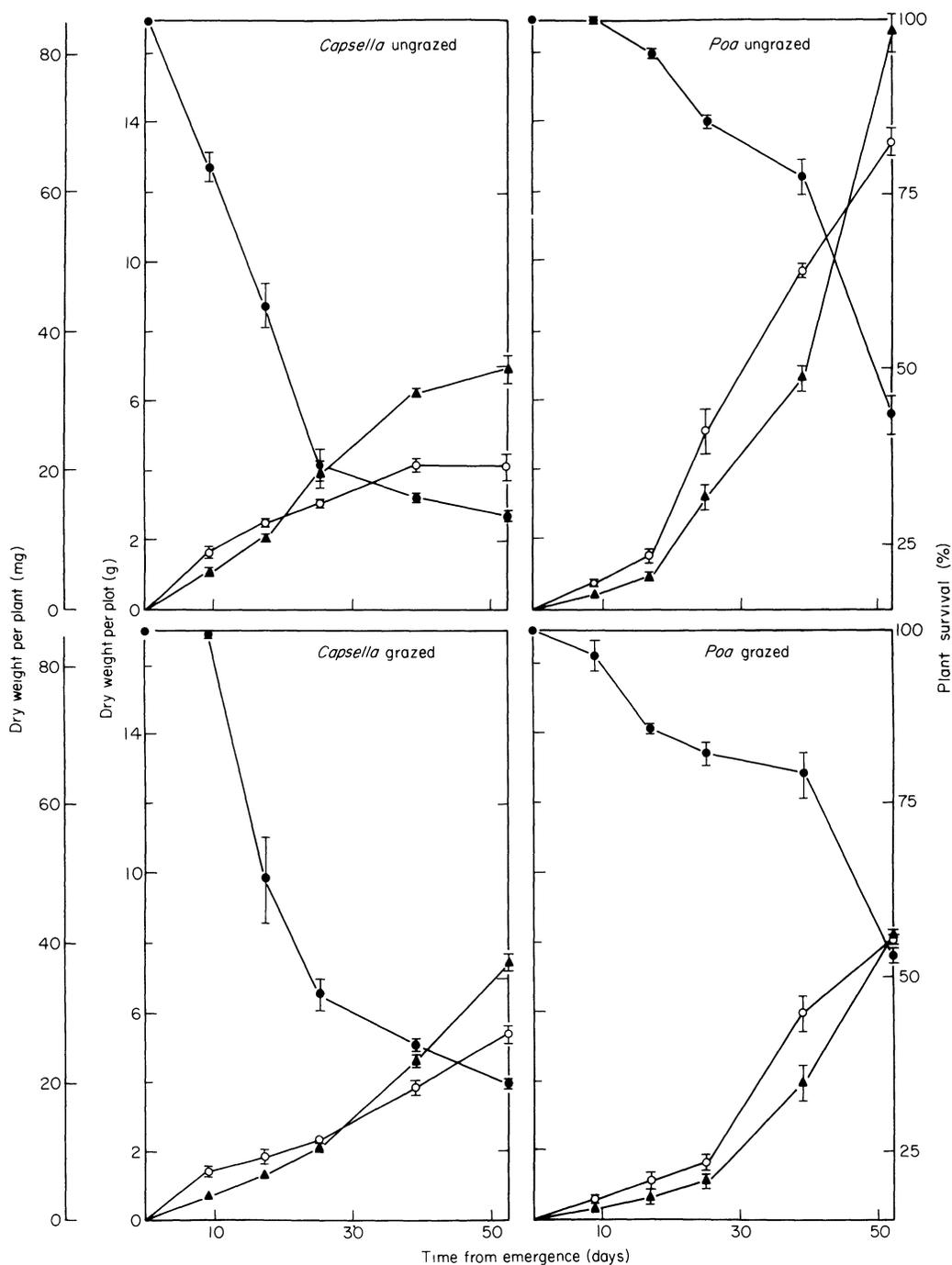


FIG. 1. The growth and survival of plants of ungrazed and grazed populations of *Capsella bursa-pastoris* and of *Poa annua* (mean of two replicates and range); ●, plant survival (%); ○, dry weight per plot (g per/340-cm² tray); ▲, dry weight per plant (mg).

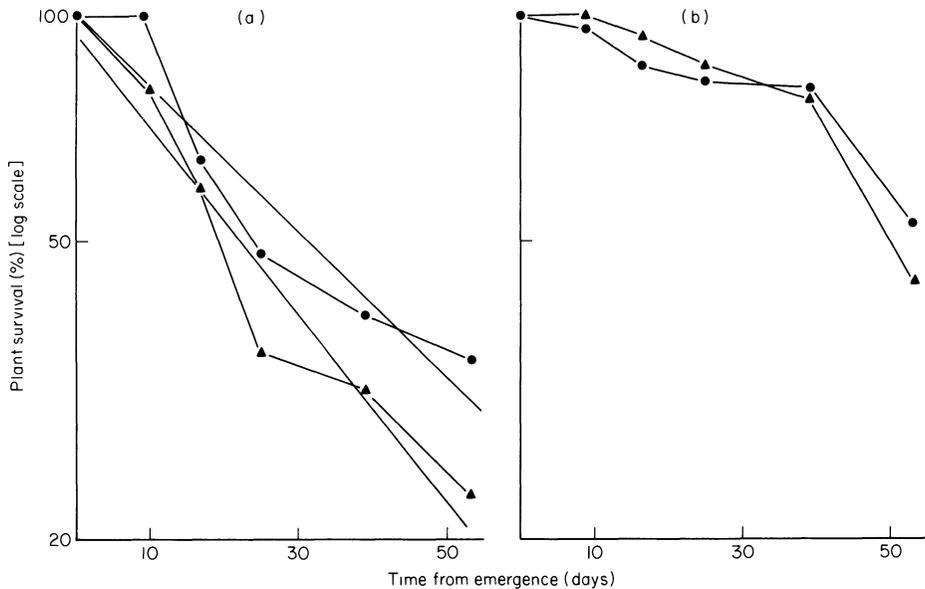


FIG. 2. The time-course of survival of plants of (a) *Capsella bursa-pastoris* and (b) *Poa annua* in grazed and ungrazed populations. The fitted linear regressions for *Capsella* are shown as straight lines: \blacktriangle , ungrazed; \bullet , grazed.

were lost from the population at a constant rate) and the risk of death was much greater than in *Poa* in which it remained low and constant until H4 and then increased rapidly. The death risks in the populations of the two species are readily interpretable in relation to the yield of dry matter per tray (Fig. 1). *Capsella* plants grew quickly and ceiling yield was reached by H4. Interference between individual plants is intense within such populations and the early onset of self-thinning is not surprising. In contrast the yield of populations of *Poa* fell below those of *Capsella* until H3 but then surpassed them. A later start to intense self-thinning could therefore be expected in the populations of *Poa*.

Correlated changes of survivorship and the weight of surviving plants

The interpretation of mortality patterns as a response to the growth made by the survivors appeared even more clearly when mean plant weight, on a log scale, was plotted against density of survivors, also on a log scale (Fig. 3), in order to test the fit of the results to the $-3/2$ power law (Yoda *et al.* 1963). Populations of *Capsella* displayed a reasonably close fit to this law with a slope of -1.8 , which is not significantly different ($P > 0.05$) from -1.5 . The regression accounted for up to 96% of the variation. The arrows in Fig. 3 indicate the onset of flowering in *Capsella*. At that time both the growth rate and the risk of death are reduced so that the points on the graph representing different harvest dates come to lie close together. In populations of *Poa* the $-3/2$ power relationship did not become apparent until H4 and H5 (Fig. 3). The individual plants were not large enough to interfere with each other significantly and to cause death amongst neighbours until after H3.

The frequency distribution of individual weight

The frequency distribution of plant weight becomes positively skewed in dense populations as a hierarchical structure develops through time with a few large plants and many

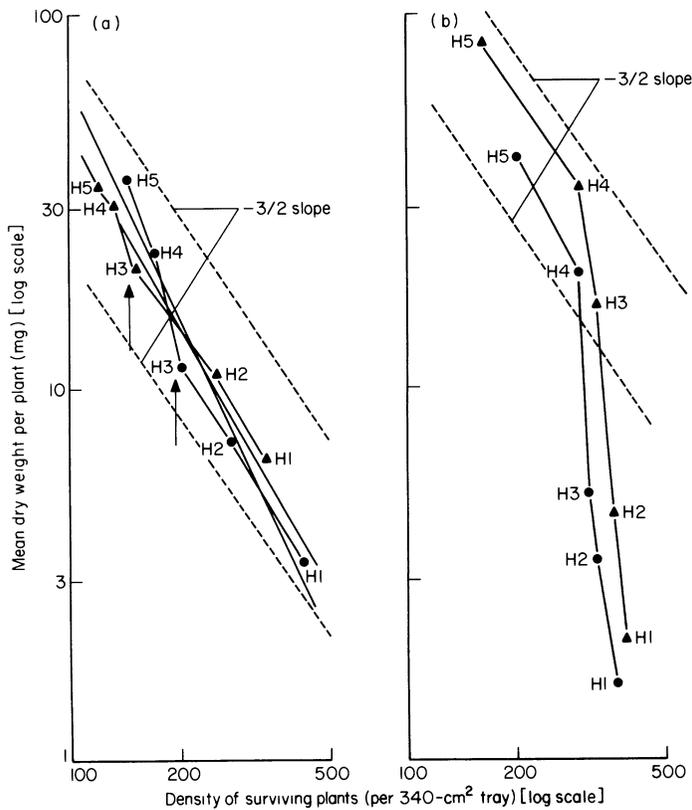


FIG. 3. Correlated changes in plant dry weight and the number of survivors in populations of (a) *Capsella bursa-pastoris* and (b) *Poa annua*. Arrows show the onset of flowering of *Capsella*. The straight lines in *Capsella* are the fitted linear regressions: \blacktriangle , ungrazed; \bullet , grazed. H1–H5 are harvest times, after 9, 17, 25, 39 and 53 days respectively.

small ones (Obeid *et al.* 1967; Bazzaz & Harper 1976). This is shown in Fig. 4 for *Poa* and *Capsella* at harvests 1, 3 and 5. The degree of skewness from normality can be quantified by g_1 , relative skewness (Zar 1974, p. 72), which is an estimator of γ_1 , the third moment about the mean of a distribution. A value of $g_1 < 0$ indicates that the sample comes from a population whose distribution is skewed to the left, while $g_1 > 0$ indicates a distribution skewed to the right. A harvest H0 was made of *Capsella* populations 4 days after seedling emergence and at that stage there was no significant departure from a normal distribution ($P > 0.05$). Skewness then developed very rapidly (Fig. 5) and departure from normality was already significant ($P < 0.01$) at H1. This is further confirmation of the very early stage at which interference develops between individuals in this species. Individual dry weight of *Poa* (Fig. 4) in contrast is normally distributed at H1 ($g_1 = 0.21$, $P > 0.05$) and significant skewness develops more slowly through H3 and H5 (Fig. 5). This again suggests that interference between individuals may be slower to develop in populations of *Poa* than in *Capsella*.

Trends of relative skewness (g_1) with time (Fig. 5) summarize the differences between the species. Skewness increases as if towards an asymptote in populations of *Capsella*—this is to be expected as the determinate growth habit involves a transition to flowering and an end of growth towards the end of the experiment. In populations of *Poa* skewness

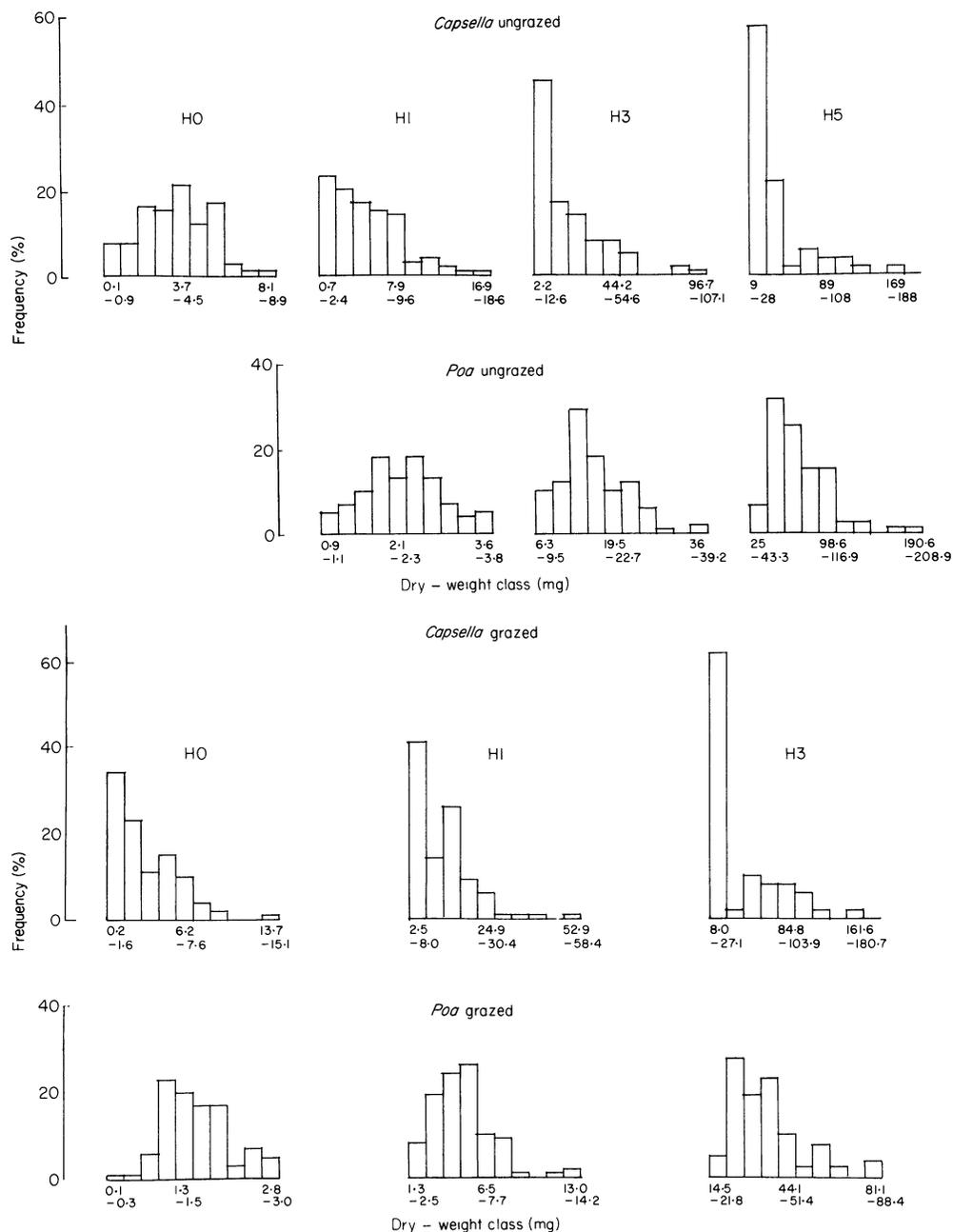


FIG. 4. The frequency distribution of dry weight in ungrazed and grazed populations of *Capsella bursa-pastoris* and of *Poa annua* at four harvest times, H0, H1, H3 and H5, after 4, 9, 25 and 53 days respectively.

is still increasing rapidly at H5, the individuals have indeterminate growth, and yield per plot was still increasing rapidly at the end of the experiment.

The behaviour of the slug-grazed populations has to be seen against this background of different growth rates, thinning regimes and frequency distributions that develop in the ungrazed populations of *Capsella* and *Poa*.

Slug-grazing on two annuals

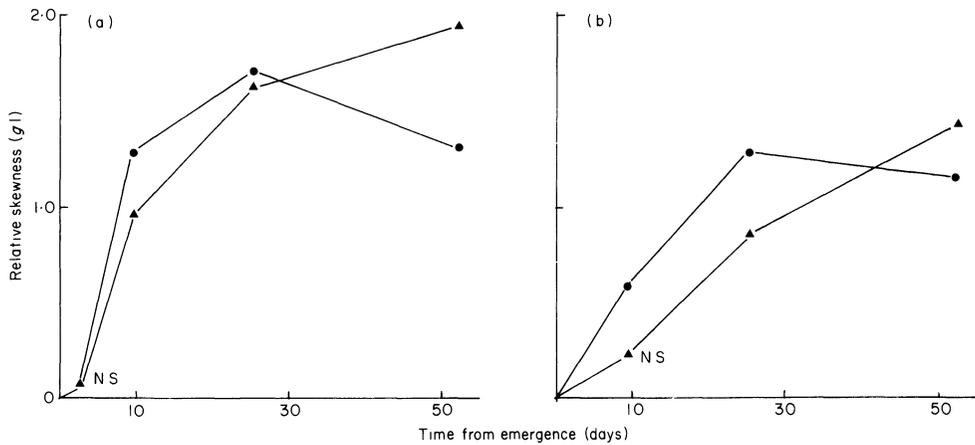


FIG. 5. The trends of relative skewness (g_1) with time in populations of (a) *Capsella bursa-pastoris* and (b) *Poa annua*. All points except those indicated as N.S. are statistically significantly different from zero at $P = 0.01$: ▲, ungrazed; ●, grazed.

Grazed populations

General features of slug damage

Capsella was readily accepted by the slugs and defoliation started on the first night of their introduction. *Poa*, in contrast, was not eaten during the first two nights but grazing started after a 'starving threshold' of c. 66–68 h.

The slugs attacked *Capsella* and *Poa* in quite different ways. Parts of the leaves of *Capsella* were eaten and sometimes whole leaves were separated from the plant as the slugs chewed through the petioles. The slugs attacked *Poa* by chewing through the young shoots at ground level. Some of the grass plants damaged in this way were marked with plastic rings to follow the consequences of this type of damage. Most often the damaged plants died quickly; in a few cases the seedlings remained alive and regenerated but died later, perhaps as a consequence of the combination of defoliation and suppression by undamaged neighbours.

The spatial pattern of damage was determined by dividing the whole of each tray into twenty small quadrats, counting the number of damaged plants in each and comparing the frequency of damage against a Poisson distribution. After 1 week of grazing the variance/mean quotient was significantly greater than 1 (Table 1) for both species indicating contagious distribution of damage, i.e. slugs tended to graze neighbouring plants. After a further period of grazing, damage became widespread through the populations, most of the quadrats contained a considerable number of damaged plants, and there was no longer evidence of clumped grazing.

TABLE 1. The spatial pattern of damaged plants in populations of *Capsella bursa-pastoris* and *Poa annua* after 1 week of grazing by the slug *Agriolimax caruanae*

	<i>Capsella bursa-pastoris</i>	<i>Poa annua</i>
Total number of damaged plants per plot	45	22
Mean (\bar{x}) per 4 × 4-cm quadrat	2.3	1.1
Variance (s^2)	14.0	4.8
Variance/mean	6.2	4.4
Significance ($H: s^2/\bar{x} = 1$)	$P < 0.001$	$P < 0.001$

Biomass production

The yield of the grazed populations is shown in Fig. 1. Dry matter production followed the same general trends as in the ungrazed populations but a comparison of grazed and ungrazed populations showed the following differences. The effect of slug grazing on the yield of *Capsella* was most marked early in development; grazed trays yielded 87 and 74% of the ungrazed trays at H1 and H2 respectively. The effect gradually decreased despite the continued presence of the slugs, and by H5 the yield of the grazed populations was not significantly different from that of the ungrazed ones ($P > 0.10$). Although *Poa* was much less acceptable than *Capsella* to the slugs, and grazing started later, the slugs caused more damage to *Poa*. Grazed populations of *Poa* yielded 30–60% of the ungrazed ones with the exception of the value 74% at H1. Despite this considerable yield reduction relative to the ungrazed populations, the grazed populations of *Poa* eventually achieved a much greater biomass than did the grazed populations of *Capsella*.

Survival

As in the controls, some individuals in grazed populations of both *Capsella* and *Poa* died (Fig. 2) but the risk of death in grazed populations of *Capsella* was conspicuously smaller than in ungrazed ones. This suggests that the activity of the slugs reduced the intensity of natural density-dependent thinning—presumably by defoliating the plants and making them smaller so that damaged plants interfered with each other less than did the vigorously growing ungrazed ones. The risk of death in *Poa* was less affected by the presence of slugs. In the period H1–H3, when there was little if any density-dependent thinning, survival was marginally higher in the ungrazed populations. In the period H4–H5 when competitive interaction had developed strongly in the ungrazed populations and self-thinning was occurring, the presence of slugs slightly decreased the death risk of the surviving grass plants.

Values for changes in the dry weight per plant (Fig. 6) complement the results for yield per plot and survival. The mean weight per plant in grazed populations of *Capsella* was consistently lower than that of ungrazed plants except at the last harvest. The weight per plant of *Poa* in the grazed populations was only slightly smaller than that of ungrazed plants at H1 and H2 but was dramatically reduced from H3 to H5.

Correlated changes of survival and individual plant weight

Patterns of thinning in the grazed populations (Fig. 3) were again analysed and tested for conformity with the $-3/2$ power law. The results were essentially similar to those obtained in the ungrazed populations. Self-thinning in *Capsella* (Fig. 3) gave an exponent of -2.2 which does not differ significantly from -1.5 ($P > 0.05$). The regression accounted for up to 92% of the variation. Anomalous values occurred after the onset of reproduction (see arrow in Fig. 3) when the growth rate and risk of death both declined. If analysis is carried out eliminating the results for the following period (H4–H5) a slope of -1.6 is obtained which does not depart significantly from -1.5 ($P > 0.05$). The interpretation of self-thinning in grazed populations of *Poa* (Fig. 3) is the same as for the ungrazed populations: density-dependent thinning is delayed until H4 when the plants are large enough for individuals to interfere with each other. The values at H4 and H5 conform reasonably closely to the expected slope of $-3/2$.

The frequency distribution of individual plant weight

Analysis of the frequency distribution of dry weight (Fig. 4) was made at harvests 1, 3 and 5 (Fig. 5). Populations of *Capsella* showed a significant departure from normality at all

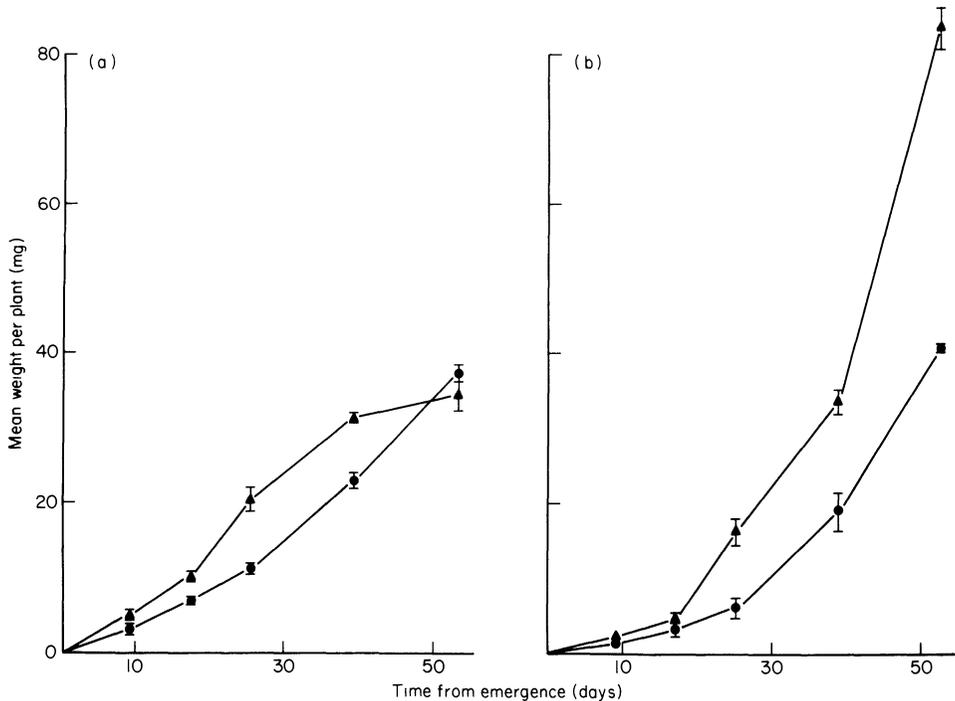


FIG. 6. Growth in dry weight per plant in populations of (a) *Capsella bursa-pastoris* and (b) *Poa annua* (mean of two replicates and range): ▲, ungrazed; ●, grazed.

harvests (except H0). At H1 the populations of *Poa* showed a weak though significant tendency to depart from normality ($g_1 = 0.58$, $P < 0.01$), which perhaps reflects an alteration of the population structure by slug damage rather than by density or sampling bias. At H3 and H5 departures from normality remained significant ($P < 0.01$).

Trends of the statistic g_1 (relative skewness) with time (Fig. 5) show a general tendency for initial increase and later approach to an asymptote although the populations of *Capsella* show a reduced value of g_1 at H5.

Effects of slug grazing on reproduction and tillering

Observations of the number of tillers in *Poa* were made at harvests 4 and 5 (Table 2). In the grazed trays, the number of tillers increased both per plant and per tray, at both harvests, though the effects failed to reach significance at $P = 0.05$. Some plants of *Capsella* had started to flower at H3 (Table 3), but no plants of *Poa* flowered until the end of the study (H5). Flowering in *Capsella* was slightly delayed by grazing, but the effects on fruiting were more marked (Table 3). At H5, 59% of the ungrazed plants bore developing capsules compared with 21% of the grazed plants. Few plants of *Poa* had flowered at H5, but grazing appeared to delay flowering in this species also.

TABLE 2. The number of tillers produced by grazed and ungrazed populations of *Poa annua* at two harvests; mean values (range)

Harvest time (days)	Grazed		Ungrazed	
	Total per tray	Per plant	Total per tray	Per plant
H4 (39)	806 (866-745)	2.7 (2.8-2.6)	687 (694-680)	2.4 (2.4-2.3)
H5 (53)	706 (741-671)	3.6 (3.6-3.5)	563 (568-557)	3.5 (3.7-3.2)

TABLE 3. Flowering and fruiting in grazed and ungrazed populations of *Capsella bursa-pastoris* and *Poa annua* at three harvests (H3–H5); values given are for the mean number of plants, \bar{x} , flowering or fruiting (with range) and the same values expressed as a percentage of the number of plants surviving at each harvest

Harvest time (days)	Species	Grazed populations				Total	
		Flowering \bar{x} (range)	%	Fruiting \bar{x} (range)	%	\bar{x}	%
H3 (25)	<i>Capsella</i>	0.5 (1–0)	0.3	0	0	0.5	0.3
H4 (39)	<i>Capsella</i>	6.5 (9–4)	3.8	8 (10–6)	4.8	14.5	8.6
H5 (53)	<i>Capsella</i>	18.0 (24–12)	12.4	30 (31–29)	20.7	48.0	33.0
	<i>Poa</i>	2.0 (3–1)	1.0	0	0	2.0	1.0
		Ungrazed populations					
H3 (25)	<i>Capsella</i>	7 (8–6)	4.8	0	0	7	4.8
H4 (39)	<i>Capsella</i>	15 (16–14)	11.3	20 (22–18)	15.0	35	26.3
H5 (53)	<i>Capsella</i>	15 (20–10)	12.8	54.5 (67–42)	46.2	69.5	59.0
	<i>Poa</i>	11 (13–9)	7.1	0	0	11.0	7.1

DISCUSSION

In laboratory tests in which leaf discs of various plant species had been offered in Petri dishes to the slug *Agriolimax caruanae* (Dirzo 1977) there was a strong dietary preference for *Capsella*, and *Poa* was eaten only after a 'starving threshold' of *c.* 66 h. In the present study in which free-ranging slugs were offered actively growing populations of *Capsella* or *Poa*, *Capsella* was eaten readily and there was a similar 'starving threshold' before the animals would eat *Poa*. The similarity of slug behaviour in the two situations is important as it implies that the results of leaf disc experiments have validity beyond the Petri dish in which they were made. However, the effects of slugs grazing on the two plant species were quite different. The slugs ate whole, or parts of, leaves of *Capsella*, but rarely, if ever, killed the plants. In the case of *Poa*, they chewed through the young shoots at ground level, 'felling' but not consuming the leaves or shoots. Some damaged plants died, some showed slight regeneration but died later, and a few of them remained alive but stunted. A similar sort of damage was caused by the slug *Agriolimax reticulatus* grazing on *Lolium perenne* (Hatto & Harper 1969). The effect of slugs was therefore generally, in the case of *Capsella*, to change the size of plants but not their density and, in the case of *Poa*, to change the density of plants rather than their size, at least in the early phases of the study. Despite the different effect that slugs had on the two food plants, populations of both species responded to plant density by reasonable conformity to the $-3/2$ power law. In control populations of both *Capsella* and *Poa*, self-thinning occurred within the populations—there was both density-dependent mortality and density-dependent plasticity. Grazing by slugs substituted for death or plastic change that would have been produced by density alone (Fig. 2). It appears that slug damage simply removed, or reduced the size of, individuals that would have been affected by the more intense interference between individuals in the absence of grazing. The substitution of one cause of plant death or plastic change by another in this study has much relevance to interpreting field experiments in which the activity of herbivores is measured using exclosures (see for example, Harper (1977), p. 433). Changes that occur in exclosure plots will represent

not only the results of preventing grazing but also the consequent increased extent of interference that occurs between the ungrazed plants. This will almost inevitably mean that enclosure experiments underestimate the direct effects of herbivores on both biomass and species composition.

The generality of the $-3/2$ power law has been demonstrated for a wide variety of plant species and monospecific populations. It has also been shown to hold true for a mixture of two species (Bazzaz & Harper 1976). The present study extends this generalization to include monospecific plant populations in the presence of predators. An obvious next stage in development of this type of study would involve introducing predators to naturally thinning mixed populations of two or more plant species.

The effects of a predator on plant survival and dry weight represent only elements in its effect on plant fitness, which must take account of whole life histories. The present study was not specifically designed to look at this effect but differences in the reproductive behaviour of grazed and ungrazed populations emerged quite clearly in the delayed reproduction of grazed plants of *Capsella* (Table 3). A similar delay in the onset of reproduction consequent on defoliation has been observed by Collins & Aitken (1970) in *Trifolium subterraneum* where defoliation delayed flowering by as much as 30 days.

Most notably, the experiments show that slugs attack different species of plants in quite different ways and with quite different consequences. If we are to ascribe changes in vegetation to the activity of herbivores it is insufficient to measure just the amount of plant material taken or the relative acceptability of the available species. The precise form that the damage takes may override these other considerations in determining how much harm is done to the plants.

Further studies are needed to examine the response of plant populations at different density to the presence of a herbivore with both search range and the amount of interference between neighbouring plants varied. Studies are also needed of the behaviour of herbivores such as slugs in mixed plant populations where the interspersing of acceptable and unacceptable plants may modify the amount of damage that is done, and in which conditioning or habituation of slugs to available food plants may perhaps influence what is eaten and what is not.

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