

The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*

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Summary. The interaction between grazing by *Gastrophysa viridula* and interspecific plant competition was investigated for *Rumex obtusifolius* growing in the field. During an eight-month growing season non-competing *R. obtusifolius* grew larger than competing plants although herbivore loads (beetle productivity per unit leaf area) were similar for competing and non-competing plants. However, grazing significantly reduced the growth of *R. obtusifolius* only in competing plants thus demonstrating a synergism between plant competition and invertebrate herbivory. The relevance of these findings for the distribution of plant species is discussed.

Key words: Grazing – Plant competition – Growth – *Gastrophysa* – *Rumex*

It is frequently asserted that grazing by invertebrate herbivores has a much greater effect on food plants when the plants are subject simultaneously to other forms of stress such as competition or disturbance (Harper 1969; Harris 1973; Whittaker 1979). Moderate levels of herbivory may then be sufficient to alter the probability of survival of food plant species and this in turn may influence the species diversity of terrestrial plant communities (Brown 1982; McBrien et al. 1983).

However, although this is now a widely accepted view (Crawley 1983), much of the evidence which supports it has emerged from experiments conducted in the laboratory (Windle and Franz 1979; Sibma et al. 1964; Fowler and Rausher 1985). There is a clear need for such evidence from experiments in the field. Following the laboratory experiments of Parkinson et al. (1979), Newell (1984a, b) was able to show by laboratory and field experimentation that the distribution of two species of fungi in a coniferous woodland could be explained by differential grazing by *Collembolans*, and Cottam (1984) showed that grazing by slugs could alter the balance of competition between *Trifolium repens* L. and *Dactylis glomerata* L. in artificially established swards out-of-doors.

Bentley and Whittaker (1979) investigated the effects of grazing by the chrysomelid beetle *Gastrophysa viridula* Degeer on competition between two of its food plants, *Rumex obtusifolius* L. and *Rumex crispus* L. But a much more natural form of competition for *Rumex* is with surrounding grass

species. Therefore, in this study we examined the interaction in the field between grazing by *Gastrophysa viridula* (hereafter referred to by generic name only) and interspecific plant competition involving *R. obtusifolius* and swards of *Festuca rubra* L. and *Agrostis tenuis* Sibth.

R. obtusifolius is widespread throughout the U.K. being common to waste and disturbed ground, borders, hedgerows and it is a persistent weed of agricultural land. A full description of the biology and ecology of *R. obtusifolius* is given by Cavers and Harper (1964). *Gastrophysa* is a small (8 mm long approx.), metallic green, leaf-eating beetle. Adults and larvae live and feed on members of the genus *Rumex* although other members of the Polygonaceae are sometimes exploited (Remaudiere 1948). Other aspects of the biology and ecology of *Gastrophysa* were discussed by Smith and Whittaker (1980a, b).

Materials and methods

The experiment was set up in an area of unmanaged grassland on the campus of the University of Lancaster which contained a mixture of grass and dicotyledonous species and a low density population of *Rumex* spp. The experiment used a factorial design which incorporated two levels of grazing by *Gastrophysa* (grazed or ungrazed) and two levels of interspecific competition for *R. obtusifolius* (competing or non-competing with grasses). Ten replicates of each treatment were allocated equally and randomly between two blocks. Each replicate consisted of a one metre square plot which had been dug 30 cm deep, lined around the edge with polythene and filled with 10 cm of coarse sand and 20 cm of John Innes No. 2 potting compost. Plots with a competing treatment were sown with 50 g of high quality lawn seed on 15 April 1983 which comprised 90% *Festuca rubra* L. and 10% *Agrostis tenuis* Sibth. Plots without a competition treatment were hand-weeded throughout. *R. obtusifolius* seeds were germinated and grown in a glasshouse and transferred outside to harden-off prior to transplanting. Four *R. obtusifolius* plants of roughly the same size were transplanted in a well spaced pattern into each of the plots on 12 May 1983.

Large numbers of *Gastrophysa* were reared on *R. obtusifolius* in the laboratory (see Speight 1983) and two females and two males were released onto each grazed plot on day 1 (1 June 1983). In order to ensure that cohorts of *Gastrophysa* were established on all grazed plants simultaneously the grazed plots were inspected after one week to ensure that

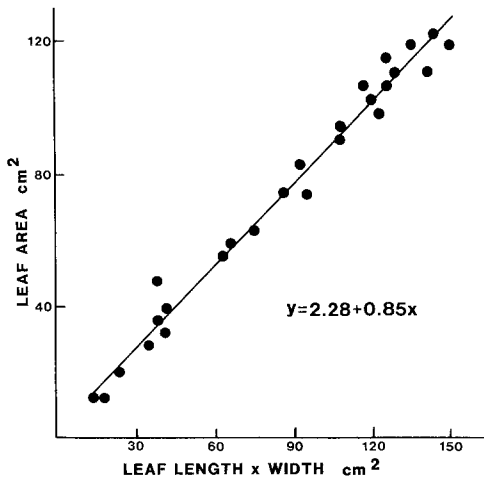


Fig. 1. Principal axis equation of *Rumex obtusifolius* leaf area (cm^2) as a function of the product of leaf length and leaf width (cm^2) used to estimate the total leaf area of plants in the field. The correlation coefficient, $r=0.99$ ($P < 0.001$; d.f. = 23)

females were still present and/or eggs had been laid, and if not a further two gravid females were added. Thereafter no further additions of *Gastrophysa* into the experimental system were made.

In addition to a final harvest of *R. obtusifolius* its growth was estimated during the season. This was achieved by measuring the length and width of all leaves on a randomly selected plant in each plot on day 1, day 16 and then about every thirty days up to day 140. These data were used to calculate the total leaf area per plant using an independently derived Principal Axis equation between leaf area and the product of leaf length and leaf width (Fig. 1). To allow for the consumption of foliage by *Gastrophysa* and other herbivores the calculated area for each leaf was corrected by estimating by eye the percentage area missing. The above-ground parts of the selected plants in each plot were harvested on day 140. Leaves and petioles were detached, separated, dried at 80°C and weighed. Final leaf areas were also measured on an electronic planimeter. The overwintering rosettes and roots were similarly harvested on 17 January 1984.

The numbers present of common invertebrate species on the shoots of all *R. obtusifolius* plants were counted on day 7 and then roughly every ten days until there were no *Gastrophysa* remaining (day 140). The numbers of eggs, each larval instar and adults of *Gastrophysa* were recorded. *Gastrophysa* pupates in the soil and so the pupae could not be counted. In an experiment of this kind using a mobile herbivore and a randomised field plot layout it was impossible to prevent some *Gastrophysa* from migrating out of 'grazed' plots onto 'ungrazed' plots. In order to overcome this problem in a systematic and unbiased way the ungrazed plots were inspected additionally every three or four days and any eggs or larvae found in these plots were destroyed. Adult beetles were removed and returned to the nearest grazed plot from where it was assumed they had emmigrated. Any errors which were introduced from using this procedure were assumed to be small as by far the greatest grazing damage was caused by *Gastrophysa* larvae rather than adults.

Results

Figure 2 shows the mean estimated total leaf area per plant in each treatment throughout the season. Although all plants started at approximately the same size, non-competing *R. obtusifolius* quickly grew much larger than interspecifically competing *R. obtusifolius*. Grazing by *Gastrophysa* appeared to reduce the total leaf areas of both competing and non-competing plants but the estimates of leaf area were too variable for this to be significant. To correct for skewed data and heterogeneous treatment variances, data were transformed by taking logarithms and the geometric means are given in Table 1. The initial sizes of *R. obtusifolius* measured as leaf area per plant were not significantly different. At the final harvest the effects of interspecific competition alone significantly reduced total leaf area, total leaf dry weight, total petiole dry weight, total root dry weight and total rosette dry weight (L.S.D. at $P=0.05$). Grazing by *Gastrophysa* had no additional effect on the growth of non-competing *R. obtusifolius* but grazing significantly reduced the leaf area, leaf dry weight and petiole dry weight of competing plants. The data show that interspecific competition reduced the numbers of leaves and petioles produced but not their individual dry weights. In contrast, grazing reduced dry weight per leaf (by 41%), dry weight per petiole (by 38%) and area per leaf (by 34%).

Figure 3 shows the mean total numbers of *Gastrophysa* per plant on competing and non-competing *R. obtusifolius*. At nearly all census dates the numbers of *Gastrophysa* were greater on non-competing plants. The peaks of the curves in Fig. 3 indicate that there were three generations of *Gastrophysa* produced on non-competing plants but only two generations on competing plants. *Gastrophysa* was not recorded on competing plants after early September whereas it persisted on non-competing plants into October.

In an experiment lasting eight months it is difficult to make useful comparisons of herbivore load on the basis

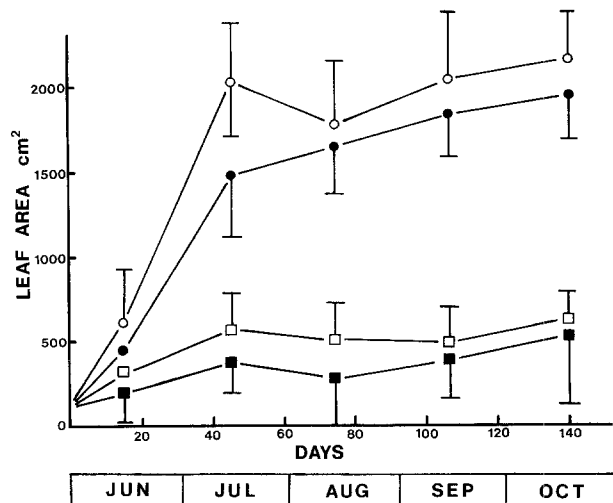


Fig. 2. Mean estimated total leaf area per plant of *Rumex obtusifolius* (cm^2) grown in the field in a factorial experiment with two levels of competition and grazing. Estimates of leaf area were made using the equation shown in Fig. 1. Vertical bars represent the standard error of each mean estimate. (○—○) = non-competing/ungrazed, (●—●) = non-competing/grazed, (□—□) = competing/ungrazed, (■—■) = competing/grazed

Table 1. Final harvest data for *Rumex obtusifolius* grown in the field in a factorial experiment with two levels of competition and grazing. Each value is the geometric mean dry weight or area of ten replicates. Means which do not share the same superscript are significantly different in the LSD (0.05) test performed on transformed data

Variante	Competing		Non-competing	
	Grazed	Ungrazed	Grazed	Ungrazed
Initial leaf area plant ⁻¹ , cm ²	133.6 ^a	144.8 ^a	150.7 ^a	137.6 ^a
Final leaf area plant ⁻¹ , cm ²	177.7 ^a	454.9 ^b	1844.6 ^c	1826.2 ^c
Leaf dry weight plant ⁻¹ , g	0.6 ^a	1.6 ^b	6.9 ^c	6.6 ^c
Root dry weight plant ⁻¹ , g	12.5 ^a	15.9 ^a	81.6 ^b	101.2 ^b
Rosette dry weight plant ⁻¹ , g	1.7 ^a	2.2 ^a	6.8 ^a	7.9 ^a
Petiole dry weight plant ⁻¹ , g	0.3 ^a	0.8 ^b	2.0 ^c	2.0 ^c
Area leaf ⁻¹ , cm ²	67.4 ^a	101.4 ^b	110.9 ^b	116.8 ^b
Dry weight leaf ⁻¹ , g	0.2 ^a	0.3 ^b	0.4 ^b	0.4 ^b
Dry weight petiole ⁻¹ , g	0.1 ^a	0.2 ^b	0.1 ^{ab}	0.1 ^{ab}
Number leaves plant ⁻¹	3.0 ^a	4.6 ^a	17.2 ^b	15.7 ^b

Table 2. Mean production of *Gastrophysa viridula* per plant (mg dry weight plant⁻¹ interval⁻¹) calculated between successive census dates for interspecifically competing and non-competing *Rumex obtusifolius*

Census dates (from 1 June 1983)	Production	
	Competing	Non-competing
1	0.0	0.0
7	3.6	9.6
17	2.6	12.5
28	7.7	21.0
37	6.4	28.7
48	7.0	13.0
57	2.0	26.7
68	2.6	55.6
78	6.6	69.1
90	2.4	12.2
103	6.0	7.2
114	0.0	0.8
140	0.0	0.0

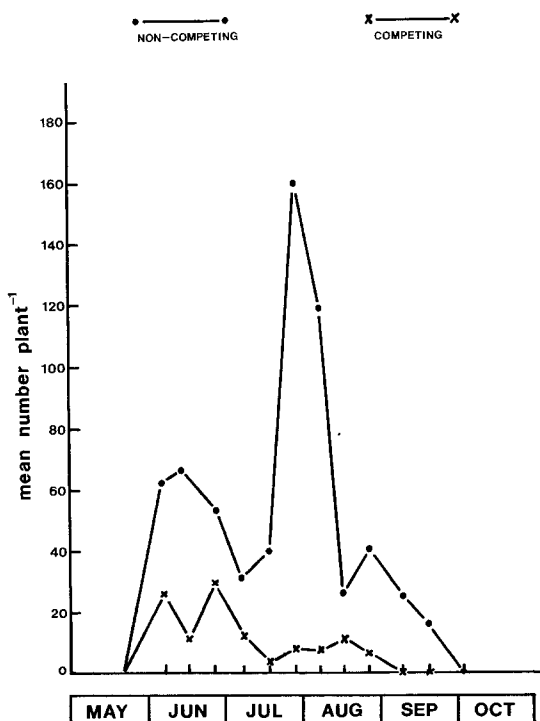


Fig. 3. Mean total numbers per plant of *Gastrophysa viridula* on interspecifically competing and non-competing *Rumex obtusifolius* at regular census dates throughout the summer of 1983

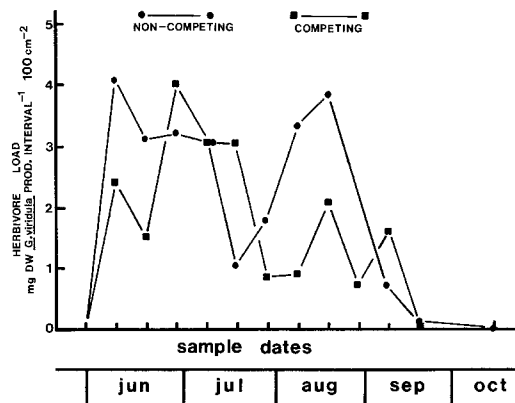


Fig. 4. Mean herbivore load of *Gastrophysa viridula* (mg dry weight 100 cm⁻² of leaf interval⁻¹) on interspecifically competing and non-competing *Rumex obtusifolius* during the summer of 1983

of straightforward standing crop measurements. For example, if we assume that herbivore production is directly related to consumption then productivity will be a useful measure of the potential effect of the herbivore on the food plant. Table 2 shows the production of *Gastrophysa* on *R. obtusifolius* during the season expressed as mg *Gastrophysa* dry weight produced during each census interval. The method for estimating productivity is given in Appendix 1. However, in order to correct for plant size differences a standardised measure of herbivore load was calculated as the mean productivity of *Gastrophysa* during each census interval per unit leaf area for competing and non-competing plants (Fig. 4). The mean leaf areas of *R. obtusifolius* at each census date were interpolated by fitting logistic curves to the data in Fig. 2. In each case curve fitting removed over 90% of the variation in leaf area. The productivity of *Gastrophysa* between each census is given in Table 2. Despite the apparent differences in *Gastrophysa* populations (Fig. 3) and productivity (Table 2) it would appear that the herbivore loads

on competing and non-competing plants were not markedly different although the herbivore loads on non-competing plants may have been slightly larger during the second half of the season. It would seem that larger non-competing plants supported *proportionally* larger herbivore populations.

The only other invertebrate species which achieved substantial abundance was the dock aphid, *Aphis rumicis* (L.). During the mid-summer, very large infestations developed on some plants but not on others. Although the aphids were not evenly distributed over the experiment there was no indication that the aphids favoured the plants of any particular treatment combination. To prevent infested plants from being badly damaged *Aphis rumicis* was removed by hand throughout the rest of the season. The remainder of the invertebrate herbivore community associated with *R. obtusifolius* consisted mainly of the spittle bug, *Philaenus spumarius* (L.); weevils (Curculionidae) notably *Apion* spp.; larvae of the Lepidoptera and Symphata; and species of slugs and snails, notably *Deroceras reticulatum* (Muller).

Discussion

Laboratory studies of the effects of grazing by *Gastrophysa* resulted in a greater reduction in the growth of *Rumex crispus* L. compared with *Rumex obtusifolius* (Bentley and Whittaker 1979). In addition, *R. crispus* responded to grazing with a decrease, and *R. obtusifolius* with an increase, in the root:shoot biomass ratio. When the two species were grown together in pots in the glasshouse these effects conferred a competitive advantage on *R. obtusifolius*. In the field, grazing resulted in fewer and lighter seeds of *R. obtusifolius* (Bentley et al. 1980) which may give rise to competitively weaker seedlings with reduced survivorship (Cideciyan and Malloch 1982). Also, the diversion of biomass away from the roots in grazed *R. crispus* led to a higher mortality of plants on a shingle bank which experienced flooding (Whittaker 1982). In this study, grazing by *Gastrophysa* in the field reduced the growth of *R. obtusifolius* only when grazing was accompanied by intense interspecific competition; thus demonstrating a synergism between plant competition and herbivory.

This result may at first seem surprising because interspecifically competing *R. obtusifolius* supported less numerous, less persistent and fewer cohorts of *Gastrophysa* compared with non-competing plants. These results concur with those of Smith and Whittaker (1980a) who showed that the number of generations and larval survival of *Gastrophysa* were reduced in floristically diverse habitats. However, as Fig. 4 shows the herbivore loads both of competing and non-competing *R. obtusifolius* as defined here would seem to be unaffected by the floristic complexity of the habitat. The effects of habitat diversity on the herbivore loads of plants have been intensively studied (Stanton 1983) but there have been few attempts to define herbivore load precisely and to correct for the variability in the size of plants from different habitats. Previous studies have used herbivore number per unit leaf area (Pimental 1961; Bach 1984) or herbivore biomass per unit plant biomass (Root 1973) to standardise comparisons of herbivore loads. However, these estimates are primarily a function of herbivore standing crop and do not account for the turnover of herbivore biomass on the plant. It is herbivore turnover or productivity

which is more likely to be correlated with the damage sustained by a plant. It is suggested that the definition of herbivore load used here (biomass produced leaf area⁻¹ interval⁻¹) is a more precise and ecologically meaningful parameter. More comparative studies using a standard measure of herbivore load need to be performed before any robust generalisations can be made about the effects of vegetation diversity on plant-invertebrate interactions.

It is interesting to note that current ecological theory predicts that plants grown in polyculture will support smaller herbivore loads and suffer less damage compared with plants grown in monoculture (Root 1973; Strong et al. 1984). The results presented here suggest that whilst this may be true for herbivore numbers it may not apply to herbivore load and that, in any case, herbivore load *per se* is not necessarily an accurate predictor of the effects of invertebrate herbivores. Rather the response of a plant to a given herbivore load will be determined by other factors which impinge on the growth of the plant. For example, competition, disturbance, drought etc., may lead to increased herbivore attack perhaps because of the increased nitrogen content of plants subject to these stresses (White 1984). Clearly, invertebrate herbivory cannot be considered in isolation from other ecological factors. Harper (1982) suggested that further progress in understanding the distribution of plants might be made by asking 'not what it is about an organism that enables it to live where it does, but what are the limits and constraints that prevent it from living elsewhere?'. To that end it is important not to overlook the interactions between inconspicuous levels of invertebrate herbivory and plant competition which could lead to the exclusion of a plant species from a given habitat.

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Appendix 1. The production of *Gastrophysa* between each census was calculated using age-class data averaged over all *R. obtusifolius* plants in each treatment. The data were partitioned into cohorts using Fig. 3 as a guide. Productivity was calculated by summing (i) the increase in standing crop and (ii) the biomass of individuals that died, emigrated or were predated. It was not practicable to measure the biomass of exuviae, respiratory losses or pupae.

Let N_t, N_{t+1} = the mean number plant⁻¹ of *Gastrophysa* at t and $t+1$ in each cohort.

W_t, W_{t+1} = the weighted means of individual *Gastrophysa* dry weights in each cohorts at t and $t+1$.

The dry weight of eggs (0.025 mg); first (0.63 mg), second (1.5 mg) and third (3.09 mg) instars; adult male (2.5 mg) and females (6.8 mg) were determined from laboratory cultures. (i) was estimated by:

$$N_{t+1} \cdot (W_{t+1} - W_t)$$

and (ii) by:

$$(N_t - N_{t+1}) \cdot \frac{W_{t+1} - W_t}{2}$$

the sum of (i) and (ii) simplifying to:

$$\frac{1}{2}(W_{t+1} - W_t) \cdot (N_{t+1} + N_t)$$

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