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The Journal of Applied Ecology, Vol. 28, No. 3. (Dec., 1991), pp. 759-776.

Journal of Applied Ecology (1991), **28**, 759–776

THE IMPACT OF ROOT HERBIVORY AS A FUNCTION OF PLANT DENSITY AND COMPETITION: SURVIVAL, GROWTH AND FECUNDITY OF *CENTAUREA MACULOSA* IN FIELD PLOTS

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SUMMARY

(1) Two inter-related experiments on the effect of root herbivory by the moth *Agapeta zoegana* on *Centaurea maculosa*, an economically important rangeland weed in North America, were done under various competitive environments to study interactions between root herbivory, plant density and competition, and to obtain information on the potential impact of this root feeder as a biological control agent.

(2) Competition with grass was the most important single factor, reducing survival of rosettes to 17% of that of the control plants and strongly limiting plant growth, biomass and fecundity of the survivors, leading to a 94% reduction in biomass and a 83% reduction in seed output per area at the end of the experiment.

(3) Increased *Centaurea* density only slightly reduced plant height, survival and fecundity under the conditions studied, but significantly reduced biomass and shoot numbers per plant. However, plants at high densities produced slightly increased biomass and significantly more seeds per area than controls.

(4) Intermediate levels of herbivory had no significant impact on biomass or shoot number, either per plant or per area, but decreased plant height and reproductive mass, as well as survival of young rosettes.

(5) The intraspecific gradient of plant responses to root herbivores was found to be influenced by the competitive environment and the degree of herbivory. In nutrient-rich soils, plant reactions were well buffered from losses from intermediate levels of herbivory when plant density was low. The herbivore effect increased in plots with high density and was most detrimental when additional grass competition was present. Under competition with fescue, survival, shoot number and fecundity decreased linearly with increasing numbers of herbivores.

(6) That low levels of herbivory increased survival, shoot number and biomass per area as compared with the control plots indicates that the relation between the applied stress and the plant's response to it is not a simple one.

(7) The effect of these root herbivores as biological control agents will therefore be determined mainly by soil conditions and the competitive status of the weed. Under the generally poor soil conditions of the infested areas in North America, the main effect of *A. zoegana* on plant population dynamics will probably be through reduced rosette survival, as infested plants die relatively late in the growing season and will mainly be replaced by grass, if present.

INTRODUCTION

Centaurea maculosa Lam. (Asteraceae) was accidentally introduced from south-eastern Europe into North America, where it has become an economically impor-

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tant rangeland weed (Harris & Myers 1986). A biological control project was initiated in the early 1960s, constituting a so-called 'classical' biological control project which attempts to control an alien weed by introducing the weed's natural enemies from its area of origin. Several root-feeding insects, including *Agapeta zoegana* (Lep. Cochylidae), were recently introduced from Europe into North America for the biological control of this weed (Müller & Schroeder 1989). Successful biological control projects clearly demonstrate that phytophagous insects can reduce equilibrium plant populations well below their carrying capacities (Julien 1987), but that the effect of a biological control agent often differs greatly between habitats, depending on whether the plant is already stressed by other biotic or abiotic factors (Harris 1981; Crawley 1986). The study of effect of herbivory under various competitive environments will, therefore, provide basic information that may help to make predictions on the impact of biological control agents on weed populations more realistic.

Studies on plant responses to herbivory have received increasing attention during recent years, rekindling the debate as to whether herbivores have a beneficial, indifferent or detrimental effect on the plants they eat (Owen & Wiegert 1976; Belsky 1986, 1987; McNaughton 1983, 1986; Verkaar 1988; Crawley 1987; Owen 1990). Much of this recent controversy is based on the assumption of a constant species-specific response to herbivory. Maschinski & Whitham (1989) recently found that the probability of *Ipomopsis arizonica* (Polemoniaceae) compensating for herbivory decreased as competition with neighbours increased, as nutrient availability decreased, and the later herbivory occurred in the growing season. They therefore proposed a compensatory continuum, depending on various internal and external conditions, emphasizing intraspecific variation in compensatory responses (*sensu* Belsky 1986). Unfortunately, few studies specifically address the underlying mechanisms of a plant's compensatory response to a gradient of environmental stress factors, including herbivory. The concept of environmental stress is used here to represent 'a deviation from an "ideal" combination of factors which would be non-limiting in all classical respects' (Hunt & Nicholls 1986).

Present knowledge suggests that plant distribution and abundance may be determined largely by competitive interactions when abiotic factors are not limiting, but that selective herbivory could modify a plant's competitive ability in favour of the unattacked plant (Whittaker 1979; Crawley 1983, 1989). This assumption also constitutes the underlying principle of inoculative biological weed control (Schroeder 1983; Crawley 1983; Harris 1986; Müller 1990a). There is only limited knowledge of the interaction between competition and herbivory and their combined effect on plant performance (Whittaker 1979; Lee & Bazzaz 1980; Berendse 1985; Cottam, Whittaker & Malloch 1986; Louda, Keeler & Holt 1989). If a plant's reaction to herbivory depends on the presence or absence of additional stress factors, prediction of interactions and combined effects will be difficult (Fowler & Rausher 1985). Experimental tests are greatly needed to better understand the underlying physiological mechanisms of the observed interactive effects on plant growth and reproduction, and their ecological and evolutionary consequences. The effects of competition (Harper 1977; Weiner 1988; Grace & Tilman 1989) and defoliation (McNaughton 1983; Hendrix 1988; Crawley 1983, 1989) on plant performance and reproduction are relatively well established. However, little is known about the impact of subterranean herbivory, despite the fact that it appears to have an important impact on plant fitness and population and community structure (reviewed by Andersen 1987; Powell & Myers 1988; Brown & Gange 1989).

This is the report of a 2-year experimental study of how intra- and interspecific competition and root herbivory by *A. zoegana* simultaneously affect survival, growth and fecundity of spotted knapweed, *C. maculosa*. The hypothesis was that herbivory will be most destructive when competition is most pronounced (Belsky 1986, 1987; Louda, Keeler & Holt 1989), i.e. the hypothesis that no significant interactions exist between herbivory and competition was tested. In an experiment with potted plants of *C. maculosa*, competition with the grass *Festuca pratensis* (a common forage species) was found greatly to reduce growth and seed production. The compensatory capacity of *C. maculosa* infested by root herbivores was further greatly influenced by the level of available nitrogen in the soil (Müller & Steinger 1990).

In this study, the following questions are addressed. (i) How is survivorship, growth and fecundity of *C. maculosa* affected by the following three factors: interspecific competition with fescue, root herbivory by the moth *A. zoegana* and intraspecific competition? (ii) How important are interactions between these three factors, e.g. to what extent do the effects of herbivore damage depend on the presence or absence of competitors? (iii) What model best explains the relationship between four levels of root herbivory and the responses of *C. maculosa*, grown under high intra- and interspecific competition? (iv) What is the potential impact of *A. zoegana* as a biological control agent for *C. maculosa* in North America?

MATERIAL AND METHODS

Species

Centaurea maculosa is a biennial or short-lived perennial, comprising several subspecies ranging from western Asia to western Europe (Dostal 1976). The studied *C. maculosa* ssp. *rhenana* (Boreau) is widely distributed, occurring in eastern Europe in continental xeric plant associations, but reaches its highest densities with up to 20 plants m^{-2} in its western distribution area at ruderal sites disturbed by human activities (Müller *et al.* 1989). However, densities in abandoned or overgrazed pastures in North America well exceed 100 plants m^{-2} (H. Müller, unpubl.). The plants used in the experiments originated from seeds collected in 1986 in Lower Austria from a diploid, monocarpic, usually biennial population (Müller *et al.* 1989).

The oligophagous, facultatively multivoltine moth *A. zoegana* is widely distributed in Europe and is among the dominant species in the majority of the herbivore guilds associated with the roots of *C. maculosa* in Europe (Müller 1989a). Highest densities with up to 23·6 larvae per 100 plants were reached in eastern Austria/north-western Hungary, and less than 8 larvae per 100 plants in central Hungary and eastern France (Müller *et al.* 1989). The eggs of *A. zoegana* are laid singly, or in groups of up to three on the surface of leaves and stems of *C. maculosa*. Larvae emerge within 10 days and immediately move to the root crown area, where they start mining. Later instars form spiral mines in the cortical tissue of the taproot. In western Europe, the moth is univoltine and the main period of feeding occurs during autumn and spring (Müller, Schroeder & Gassman 1988).

Festuca pratensis, used in the experiments as a competing forage grass, is commonly associated with *C. maculosa* in the more mesic habitats in Europe. Closely related species have a potential in reseeding programmes in North America as competitors of *C. maculosa*. *Festuca pratensis* has a relatively slow development in its first year, but its competitive ability greatly increases following cutting, due to intense regrowth and the formation of stolons.

Site conditions and experimental design

The field site is located 10 km outside Basel, with a semi-humid, temperate central European climate. An uncultivated grassland field measuring 20 × 30 m was ploughed in autumn 1986 and subsequently divided into 50 1 × 1 m plots, arranged in five blocks along a slight incline. A 50-cm buffer zone around each plot was covered with granulated bark to keep grass and weeds from invading the plots, and the rest of the field was sown with a grass mixture. The soil can be characterized as a skeleton-free parabrown earth developed on loess, with an average depth of 100 cm. The top soil (0–20 cm) contains 17·1% clay, 33% silt, 40·8% sand and 3% humus, with a pH of 6·3 and 1·7% C and 0·17% N_{kj}. The soil is classified as highly fertile (Besson *et al.* 1987).

Two inter-related experiments were set up. Experiment 1 consisted of a 2 × 2 × 2 full factorial design with two knapweed densities (d/D), and root herbivores (H8/h) and grass competition (G/g) either present or absent, resulting in eight treatments. Two supplementary plots with high knapweed density and grass competition were infested with two extra levels of root herbivores (H4, H16) and included in each block. These two plots, together with the two plots from experiment 1 containing both high knapweed density and grass, form experiment 2, thus consisting of four plots varying in the level of herbivory. The resulting ten treatments were randomized within each block. In the following, experiment 1 will be referred to as the 'competition experiment' and experiment 2 as the 'herbivore gradient experiment'. The levels of the treatment factors were chosen to simulate the range of natural conditions and a potential biological control situation (grass competition).

Knapweed density

Seeds of *C. maculosa* were sown on 30 January 1987, transplanted into Jiffy pots (5 × 5 × 5 cm, filled with a mixture of sand and standard cultivation soil) on 12 February and kept in an unheated glasshouse until 12 April, when the plants were placed outdoors. Between 29 May and 6 June 1987, either 25 (d = low density), or 100 plants (D = high density) were transplanted in a regular grid into the field plots.

Grass competition

Because of poor germination in the field due to adverse weather conditions, *Festuca pratensis* var. Cosmos was resown in the glasshouse and *c.* 2500 seedlings resulting from 5 g of seeds were transplanted into each of the grass plots (G; as compared to g for plots without grass) by the end of July. The grass was carefully cut with scissors at 5 cm above the ground level and at approximately monthly intervals during the main growth period.

Root herbivores

Roots of *C. maculosa* containing final instar larvae and pupae of *A. zoegana* were collected in early June 1987 in central Hungary. Moths emerged in Basel during July and were immediately transferred to the field. During 40 days, from 1 July onwards, enclosure cages (1 × 1 × 1 m) were placed over all fifty plots. On average, differences in temperature and relative humidity between conditions inside and outside the cages were less than 5%, but the meshes reduced light intensity by *c.* 25%. Four couples were released in each of the herbivore plots of the competition experiment (H8 = intermediate level of herbivory; h = plots without herbivores), and 2 (H4 = low level) and 8 couples (H16 = high level), respectively, in the additional two plots of the herbivore gradient experiment. Moths were released in July, within 5 days for each block. Moth emergence from the plots could not be recorded in 1988 due to technical problems. It was assumed that all plants in the herbivore plots became attacked, and that the infestation level was proportional to the number of moths initially released (cf. Discussion).

Census

The experiments started in May and July 1987, when the rosettes were transplanted to the field plots and the herbivore and grass treatments applied, and finished on 12 September 1988. Measurements of knapweed performance were made on six occasions during 1987 (30 June, 26 July, 19 August, 21 September, 21 October and 20 November), and on six occasions in 1988 (31 March, 28 April, 27 May, 27 June, 26 July and 10 September). Only the central nine plants in the low density plots (d) and the corresponding nine plants in the high density plots (D), respectively, were subsequently measured (= test plants). Plant survival, length of the longest rosette leaf (as a measure of rosette size, H. Müller, unpubl.) and number and height of shoots were recorded on each sampling occasion. Five plants of each DgH and DgH8 (D: high knapweed density, g: without grass, h/H8: herbivores;absent/present) plot (randomly selected from the original thirty-six central plants, except the test plants) were carefully removed on 20 June 1988, when shoot height was at maximum. The plants were separated into above- and below-ground parts and the biomass determined (dry mass at 65 °C after 15 h).

To estimate the relative intensity of grass competition in the various grass treatments, above-ground biomass production of the fescue was determined in the central 0·36 m^2 for the period 10 October–10 November 1987 for each grass plot, by cutting and weighing the grass produced during this period. Eco-physiological parameters were assessed in the competition experiment for selected treatments only, depending on the question addressed and the number of plots available with plant numbers allowing enough replicates. Light intensity (PAR, LI-COR) was measured on 9 October in each of the five plots of the four treatments dGh, Dgh, dGh, DGh, to determine the effect of high density and grass competition. Measurements were taken on a sunny day, shortly before the fescue was cut, directly above the rosettes of each of five plants per plot, and two additional records were taken above the grass canopy before and after the measurements of each plot. To estimate the impact of grass competition and herbivory on physiological characters, transpiration and stomatal conductance of plant leaves (LI-COR, 1600 Steady State Porometer) were measured on 23 June 1988 for the Dgh, DGh and DGH treatments. Nine leaves of similar relative stem height from each of several plants were measured in each of four plots per treatment. Water potential was measured in a pressure chamber (PMS Instruments) on 26 July 1988 for the four treatments Dgh, DgH, DGh and DGH. Three to five apical pieces (5 cm) of a lateral shoot with one terminal flower head were cut off from each of 3–6 plants in each of 3–5 plots per treatment. Plant parameters at final harvest (12 September 1988) were assessed both on a per-plant and per-area ($0{\cdot}36\,m^2$) basis. All remaining plants within the central $0{\cdot}36\,m^2$ were removed and the above-ground biomass determined.

Because flower heads shed their seeds some time after maturation, all flower heads containing newly matured seeds (dried, light brownish heads) were cut and counted from the test plants at 3-day intervals from 5 August onwards until final harvest, when all remaining flower heads were removed. Reproductive characters at final harvest were assessed both on a per-plant and per-area basis. All plants within the central $0{\cdot}36\,m^2$ were removed, separated into vegetative and reproductive (i.e. flower heads) plant parts and the biomass determined at 65 °C (root mass could not be reliably assessed and was therefore excluded). Subsequently all seeds were removed from the flower heads of the test plants, weighed, and the weight of 100 seeds determined for each plant, which allowed the calculation of mean seed weight, average number of seeds per flower head and seed number per plant. Fecundity of the non-test plants was interpolated from their flower head numbers.

Analyses

The eight treatments of the competition experiment were analysed as a completely randomized block design, using ANOVAS, with the five blocks as the blocking factor and grass competition, knapweed density and root herbivory, each with two levels, as the three treatment factors. ANOVAS and regression analyses were performed to compare the four treatments of the herbivore gradient experiment. The two treatments DGh and DGH8 were thus used in both analyses. Analyses of variance for plant growth, eco-physiological characters, biomass and reproduction are all based on plot means to avoid pseudoreplications. Plant survival was analysed for each plot after angular transformation of the relative survival rates (from the original nine plants). Plant height, total shoot length (mean plant height × shoot number) and biomass were log-transformed and seed numbers square-root transformed. The number of interaction terms between the treatment factors generally decreased after transformations. In order to compare the effect of initial and final density, the analyses were also performed with final knapweed density as the covariate. As the trends were generally maintained, but became slightly less pronounced, the results of the ANOVAS only will be given.

Relative values of light intensity, as compared to the average of the two corresponding outside measurements, were calculated for the five plants of each of the twenty plots, angularly transformed and subjected to a two-way ANOVA with density and grass competition as the main factors.

All statistical analyses were carried out using the general statistical program GENSTAT 5 (Payne 1987).

RESULTS

Plant performance in 1987

Unexpectedly, 61% of all transferred rosette plants started bolting before 26 July, and an additional 10% by 19 August of the first year, probably as a consequence of the early seeding and the highly fertile soil. Probability of bolting was independent of knapweed density ($P > 0{\cdot}10$) and occurred before the grass and herbivore treatments were applied. The probability and time of bolting was, however, dependent on rosette size, measured as maximum rosette diameter (Table 1). In order to prevent seed set and subsequent death, all shoots which had bolted were cut on 5 August. Nevertheless, mortality was 76·6% by 20 November in these plants, as compared with only 35·4% of the rosette plants. The relative mortality of flowering plants that were cut, however, was independent of the treatments ($P > 0·10$), and the clipped plants were therefore included in the analyses.

The above-ground biomass of fescue produced between 10 October and 10 November did not differ significantly between plots with low and high knapweed density ($P = 0·32$; mean dG, 37·7 g; mean DG, 32·8 g).

Plant growth in 1988

Development of total shoot length from April to September 1988 is presented in Fig. 1, and corresponding growth curves were similar for the development of plant

TABLE 1. Relationship between rosette size (diameter in cm) and probability of bolting

	Plants bolting before			Plants remaining as rosettes in 1987
	6 July	26 July	19 Aug.	
Mean rosette diameter on 15 June	26.82^{a}	25.00^{ab}	24.69^{ab}	24.43^{b}
Number of plants	42	232	46	130

Means followed by the same letter are not statistically different from each other (Scheffé *F*-test, $P < 0·05$).

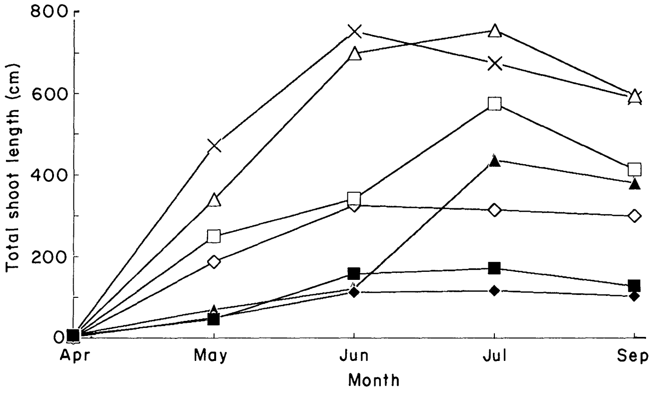

FIG. 1. Treatment effects on total shoot length (mean plant height × number of shoots) in 1987. Key: low (d) and high (D) *Centaurea maculosa* density; grass competition absent (g) and present (G); none (h) or four couples (H) of *Agapeta zoegana* released per plot; ×, dgh; △, dgH; ◇, Dgh; □, DgH; ▲, dGh; ◆, DGh; ■, DGH.

height. No measurable impact of the factors was detected in April, when the formation of the shoots started. Grass competition was the most important single factor in the analysis of variance for both growth parameters throughout the experiment, accounting for 34 and 35% of the variation in plant height and 59 and 46% of the variation in total shoot length in June and September, respectively. At the end of the growing season, herbivory also significantly decreased plant height, whereas knapweed density decreased total shoot length (Table 2). The significant interaction term for plant height resulted from the herbivore impact on plant height being more pronounced when fescue was present.

Eco-physiological characters

Average plot means for light measurements, and treatment effects on plant physiological characters are given in Table 3. The presence of the grass caused a five-fold

TABLE 2. ANOVA table on the effect of the treatment factors on growth parameters and survival at final harvest, and on survival before overwintering

Source of variation	d.f.	Plant height	Shoot length	Shoot number	Survival until Nov. 1987	Survival until June 1988
Block effect	4	0·21	0·73	16·82	312·76	235·97
Density (D)	1	0·00	13·96 ***	67·19 ***	437·73 *	19·26
Grass competition (G)	1	1·47 ***	6·53 ***	34·25 **	4221·43 ***	10671·27 ***
Root herbivory (H)	1	0·57 **	1·47	8·55	840·47 **	70·71
D * G	1	0·06	1·54	0·62	330·14	869·53 **
D * J	1	0·02	0·10	0·01	416·94 *	36·66
G * H	1	0·49 *	0·01	0·73	177·61	61·49
D * G * H	1	0·00	0·00	0·04	1207·46	122·51
Error [†]	17/17/17/28/28	0·06	6·05	54·17	2731·35	2405·87

* $P<0{\cdot}05$; ** $P<0{\cdot}01$; *** $P<0{\cdot}001$.

[†] For the various characters, respectively.

Sums of squares and significance levels of F ratios from analysis of variance of the effect of each of two levels of knapweed density, grass competition and root herbivory upon growth characters and survival of *Centaurea maculosa* (length measurements were log-transformed and relative survival rates were angularly transformed prior to analysis.

TABLE 3. Selected treatment effects (plot means) on ecophysiological characters in the competition experiment

	Low plant density		High plant density			
Treatment	gh	GH	gh	gH	Gh	GH
Light intensity (on % of full light)	0·35	0·07	–	0·21	–	0·07
Stomatal conductance cm s^{-1}	–	–	2·40	–	1·23	0·90
Water potential (bar)	–	–	−17·8	−18·9	−19·7	−20·0

Grass competition absent (g), present (G).

None (h) or four couples (H) of *Agapeta zoegana* released per plot.

reduction in light intensity ($P < 0{\cdot}001$), but high knapweed density showed no significant influence. Shoot leaves of *C. maculosa* growing in plots with fescue also showed a significant reduction in stomatal conductance as compared with fescue-free plots (one-way ANOVA with grass competition as the factor and light intensity (PAR) as the covariate, $P = 0{\cdot}022$). The presence of either grass or root herbivores slightly decreased the water potential, but neither effect was significant (grass competition $P = 0{\cdot}061$; herbivory, $P = 0{\cdot}32$).

Plant survival

Competition experiment

The effects of the treatment factors on plant survival up to November 1987, April 1988 and June 1988, i.e. the time before and after overwintering and at maximum plant height were determined by analyses of variance. Grass competition was by far the most important single factor, accounting for 40·7, 68 and 73·6% of the variance in survival of the three sampling dates, respectively, reducing survival of flowering plants to 17% of the controls (Table 2, Fig. 2). Both high knapweed density and root

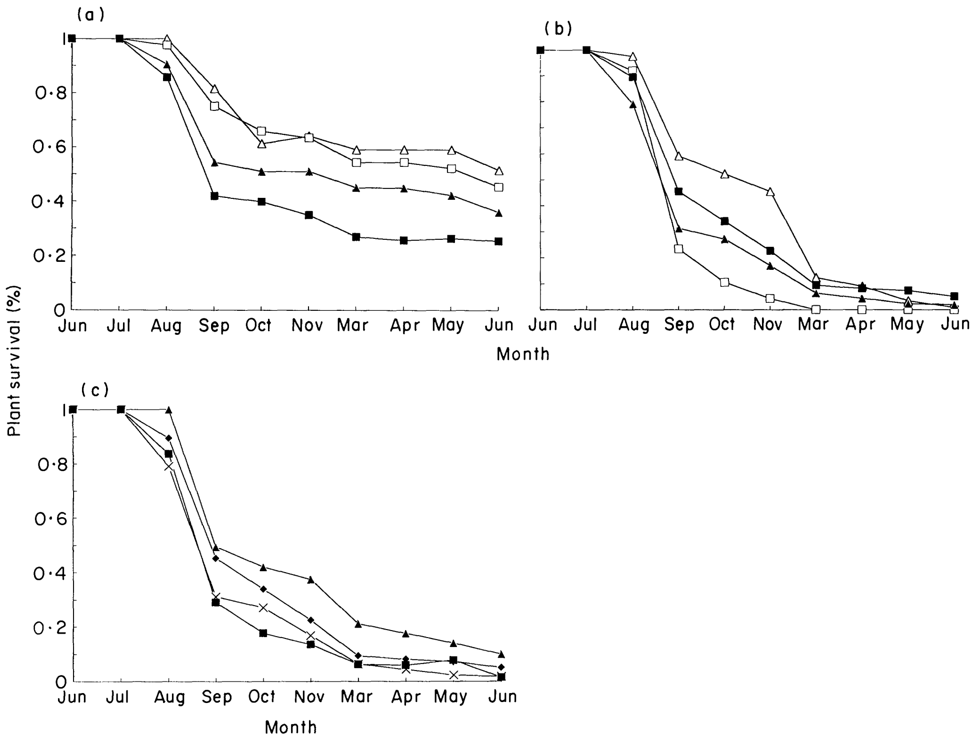

FIG. 2. Treatment effects on percentage plant survival: (a) without grass competition, (b) with grass competition, and (c) when grown under high intra- and interspecific competition with different levels of herbivory. Symbols in (c): none (h, ×), two (H4, ▲), four (H8, ◆) and eight couples (H16,■) of *Agapeta zoegana* released per plot; other treatment as in Fig. 1. Graph symbols for (a) and (b) respectively: △, dgh, dGh; □, dgH, dGH; ▲, Dgh, DGh; ■, DgH, DGH.

herbivory also significantly reduced plant survival by November 1987, but their effect decreased over time. No significant effects of these factors were observed on flowering plants, mainly as a result of the generally low survival rate. Highest plant mortality occurred during September 1987—which was mainly a consequence of cutting the bolting shoots in early August—and also during winter, together accounting for the low survival rate (Fig. 2a, b). Multiple stress generally reduced plant survival (Fig. 3a). Interestingly, however, the presence of grass reversed the effect of the interaction between density and herbivory: survival was reduced most strongly in herbivore plots with high knapweed density, when grass competition was absent, and in herbivore plots with low knapweed density, when fescues were present (Fig. 2a, b).

Herbivore gradient experiment

Surprisingly, herbivores had no influence on the survival of *C. maculosa* grown in high density and under grass competition (Fig. 2c, Table 4). However, there was a significant linear decrease in plant survival with increasing herbivore level (log-scale) on all three sampling dates (Table 4). In July 1988, survival of the flowering plants was significantly increased by low level of herbivory (H4) ($P < 0{\cdot}001$), whereas the survival in plots with intermediate (H8) and high (H16) levels of herbivory did not significantly differ from the controls (h) (Fig. 3a).

Biomass

Root biomass was slightly but not significantly increased on 20 June 1988 in the DgH8 plots as compared to the Dgh plots, and shoot and total plant biomass were slightly decreased. Herbivores, however, significantly reduced the shoot/root ratio ($P < 0{\cdot}05$; mean Dgh, 4·34, mean DgH8, 3·82).

Grass competition strongly reduced individual plant biomass and shoot number (Table 2, Fig. 3). This effect was even more pronounced on a per-area basis due to

TABLE 4. ANOVA table for the effect of the level of herbivory on plant survival and shoot number

Source of variation	d.f.	Survival unitl June 1988	Shoot number
Block effect	4	481·60	9·37
Herbivory	1	93·65	2·52 *
Level of herbivory[†]	2	327·54 **	3·76 *
Linear effect[‡]	1	327·11 **	3·33 *
Deviations[§]	1	0·42	0·43
Error	12/17	249·06	3·59

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

[†] H_0, plots with herbivores are not different from the control plots.

[‡] H_0, plots with herbivores are not different among each other.

[§] H_0, there is no linear relationship between log herbivore density and survival.

Sums of squares and significance levels of *F* ratios from analysis of variance of the effect of four levels of root herbivory (absent; 4, 8 and 16 moths released) upon survival (data were angularly transformed prior to analysis) and shoot number of *Centaurea maculosa* at final harvest.

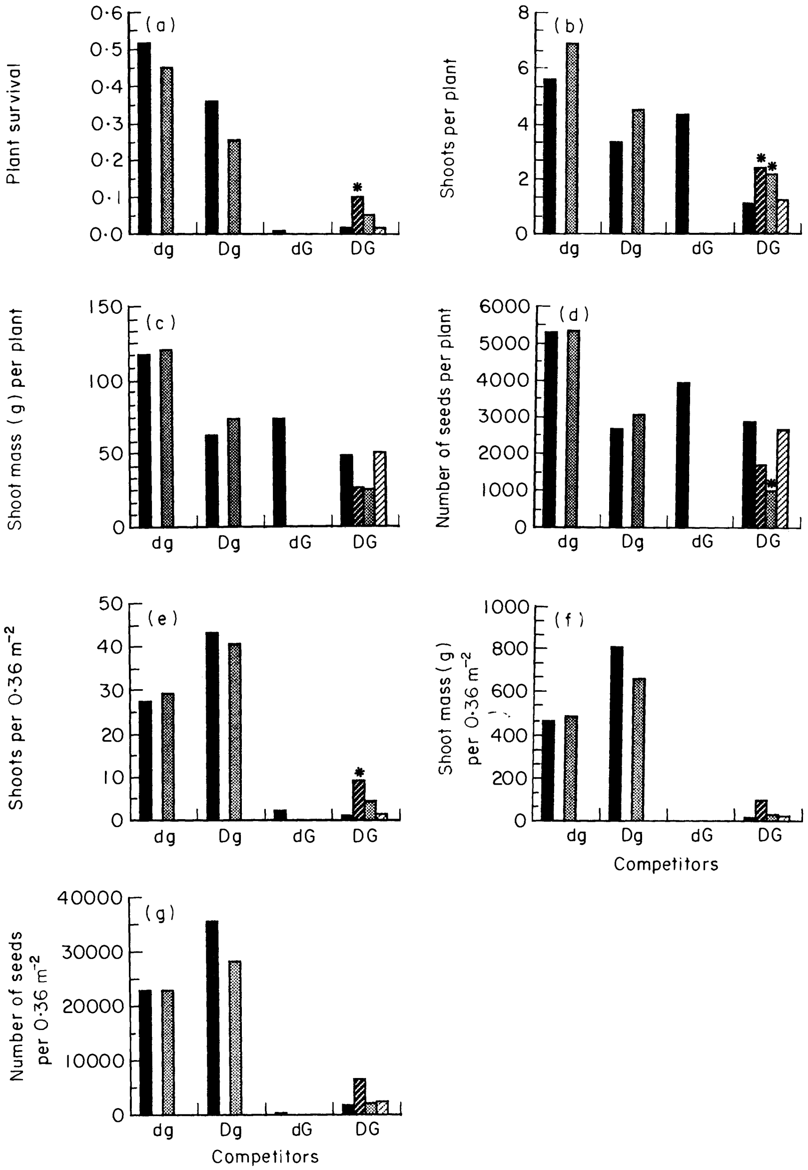

FIG. 3. The response to herbivory as a function of the plant's competitive environment: (a) survival; (b) number of shoots per plant; (c) shoot biomass per plant; (d) fecundity; (e) number of shoots $0{\cdot}36\,m^{-2}$, (f) shoot biomass $0{\cdot}36\,m^{-2}$, (g) seed output $0{\cdot}36\,m^{-2}$. Significant differences ($P < 0{\cdot}05$) between the control and corresponding herbivore plots (from two-tailed t-tests) are shown by asterisks above the columns: h, ■; H4, ▨; H8, □; H16, ▨; otherwise as in Fig. 1.

the strong effect of grass on survival. On a per-area basis, grass competition accounted for 73·2% of the variation in shoot number and 85% of the variation in biomass, reducing it to 6% of the control plots. High knapweed density also significantly reduced individual plant biomass and shoot number (Tables 2 & 5), but both parameters were increased on a per-area basis due to the increased number of individuals surviving in the high density plots (shoot mass, $P < 0{\cdot}05$; shoot number, $P < 0{\cdot}05$). The significant D * G interaction term for biomass production per area ($P < 0{\cdot}05$) is mainly due to extremely low biomass production in the dg plots, as a consequence of the low survival rate of the plants in these plots (Fig. 2a). Root herbivores had no influence on these parameters, both on a per-plant and per-plot area.

In the herbivore gradient experiment, herbivory significantly increased the number of shoots (per plant, $P < 0{\cdot}05$; per area, $P < 0{\cdot}05$), and a significant linear relationship between herbivore level (log scale) and the number of shoots for both individual plants (Table 4) and per area ($P < 0{\cdot}001$) was found among the plants where *Agapeta* was released (Fig. 3b, e). The reduction of individual shoot biomass in the herbivore treatments (H4, H8, H16) as compared with the controls (h) only narrowly missed statistical significance ($P = 0{\cdot}076$) (Fig. 3c).

Fecundity

Reproductive success was estimated by measuring total weight of flower heads and seeds and by counting their numbers. Total weight of flower heads was highly correlated with flower head number ($r = 0{\cdot}96$, $P < 0{\cdot}001$), as was seed weight with seed number ($r = 0{\cdot}99$, $P < 0{\cdot}001$). Therefore, only total weight of the reproductive structures and seed numbers are presented as response variates to the various treatments (Table 5, Fig. 3d).

Competition with grass greatly reduced reproductive output, accounting for 35 and 14% of the variation in reproductive mass and seed number per plant, respectively. This effect, together with its impact on knapweed survival, resulted on average in a 83% reduction in seed number in plots with grass competition as compared with control plots ($P \ll 0{\cdot}001$), Fig. 3g).

TABLE 5. ANOVA table on the effect of the treatment factors on shoot mass, reproductive mass and fecundity per *Centaurea maculosa* plant

Source of variation	d.f.	Shoot mass	Reproductive mass	Seed number
Block effect	4	1·23	1·28	775
Density (D)	1	1·82 *	1·39	1393
Grass competition (G)	1	5·33 **	5·14 **	2048 *
Root herbivory (H)	1	1·08	1·85 *	1057
D * G	1	0·20	0·34	580
D * H	1	0·03	0·10	18
G * H	1	1·79	2·95 *	1532
Error	17	7·53	6·69	9410

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

Sums of squares and significance levels of F ratios from analysis of variance of the effect of each two levels of knapweed density, grass competition and root herbivory upon biomass and fecundity of *C. maculosa* (dry weight was log-transformed and seed number square-root-transformed prior to analysis).

Mining by *A. zoegana* also reduced fecundity, but the effect was only significant for reproductive mass, which was most pronounced in the presence of grass (significant G × H interaction term) (Table 5). Plots with grass, high knapweed density and herbivores present showed a 35% reduction in seed number as compared to controls. All plants growing at low density and in the presence of grass and herbivores died before bolting. Root herbivory did not significantly reduce reproductive characters per area ($P \gg 0{\cdot}05$). On an individual basis, plant density only slightly and not significantly reduced reproductive mass and seed number ($P = 0{\cdot}08$ and $P = 0{\cdot}12$, respectively), but both parameters were significantly increased on a per area basis ($P < 0{\cdot}05$).

None of the treatment factors or their interaction terms showed a significant impact on mean seed weight and the variation between the treatments was less than 8%.

In the herbivore gradient experiment, no significant impact of herbivory was found on any of the reproductive variates, when plots with herbivores were compared with the corresponding control plots. In addition, no linear relationship between the level of herbivory and reproductive output could be shown among the herbivore plots. Both observations result from the fact that plants with the highest herbivore levels did not differ from the controls (Fig. 3d, g). Low and intermediate levels of herbivory, however, reduced average fecundity, with the effect of the latter being statistically significant (Fig. 3d). Despite slightly reduced seed production of plants growing in plots with low herbivore levels, these plots produced 1·75 times as many seeds per area as did the control plots, as a consequence of the increased survival rate of plants under low herbivore stress (Fig. 3g). This effect, however, was not significant due to high inter-plot variation.

DISCUSSION

The view that a single plant may express a continuum of responses to herbivory rather than a fixed response greatly improved the understanding of herbivore impact on plant performance. A cumulative model for plant responses to stress factors was proposed by Harris (1973, 1981) and the degree of a species-specific response is seen as a function of the strength of internal and external factors (Maschinski & Whitham 1989; Louda, Keeler & Holt 1989). However, there is no simple proportionality between the level of the treatment factors applied and the actual stress for the plant, as the plant's integrative response is most complex and may not be linear (Hunt & Nicholls 1986). In addition, the position of 'zero stress' (the environment promoting the maximum long-term plant performance, Hunt & Nicholls 1986) may vary from population to population and thus is difficult to assess. In the following, the effects of the treatment factors and their combinations with regard to the plant's compensatory responses will be discussed.

Effects of individual stress factors

Grass

Competition with grass was by far the most important single factor, strongly reducing survival, biomass and reproduction (plant height, total shoot length, shoot number, shoot mass, reproductive mass, seed output) which resulted in a 83% reduction in seed output per area as compared to control plots, due to combined effects on plant survival and fecundity. Under the conditions studied, *C. maculosa* is relatively susceptible to competition, thus confirming results of a parallel experiment with potted plants (Müller & Steinger 1990; Müller 1990b). Competition with grass was found to reduce the shoot/root ratio in spring, indicating that the effect of grass was mainly mediated through subterranean competition (Crawley 1983; McNaughton 1983; Tilman 1989), probably by depleting soil nutrients and water (Müller 1990b). Results of the parallel experiment with potted plants showed a substantial decline in plant available soil nitrogen when grass was present (Steinger & Müller, unpubl.). The observed reduced light intensity available for the rosette plants growing in a grass neighbourhood (Table 3) may well influence rosette size and later increase resource allocation to shoots (Hunt & Nicholls 1986). Significantly reduced stomatal conductance and slightly decreased water potential (Table 3) suggest a reduced daily period for photosynthesis and further explain the strong negative effect of grass competition on plant performance (Steinger & Müller unpubl.). The potential of a species to respond to specific stress factors may shed light on a plant's evolutionary history, assuming that a plant has optimized its resource allocation pattern with respect to the range of environments it most frequently encountered in the past. That *C. maculosa* occurs mainly in habitats with low plant cover may therefore reflect the plant's susceptibility to competition.

Density

Plants growing in the plots at quadruple density experienced increased mortality and reduced shoot number and shoot mass, yet produced slightly more seeds per area than did the plants in the low density plots (Fig. 3g). Density-dependent mortality of rosette plants and density-dependent fecundity did therefore not fully buffer the differences in initial rosette density. Hence, lowering rosette density from 100 to 25 plants m^{-2}, as may well result from competition with grass or from root herbivores, will result in reduced seed output per area.

Herbivory

The assumed relationship between the number of moths released and the number of larvae actually feeding on individual roots is based on an earlier series of experiments to test the oviposition preference of *A. zoegana* under field conditions (Müller, Schroeder & Gassman 1988). The fact that the bolting plants were cut during their exposure to the moths led to partial removal of the eggs, thus decreasing the herbivore impact. The fact that the larvae can move to another root or die when the primary resource has been depleted (Müller, Schroeder & Gassman 1988) further complicates the assessment of the actual level of herbivory of an individual plant from egg loads or plot emergence data. However, although the actual herbivore level could not be reliably assessed from the dried roots at final harvest, careful examination of selected plants from the experimental plots at the end of the experiment seems to confirm the relationship assumed above. The majority of the surviving plants exposed to *A. zoegana* showed signs of larval development, resulting from approximately 1–2 larvae, 1–4 larvae and 2–6 larvae per root, respectively, for the plants exposed to low, intermediate and high levels of herbivory.

Intermediate levels of herbivory reduced plant height and reproductive mass per plant (Table 5), but showed no significant impact on survival (except early on for rosette plants) (Table 2) and on shoot biomass, shoot number and seed output per area. Slightly increased plant moisture stress at the time of flowering and a reduced shoot/root ratio in June compared to control plants indicates an impact of herbivory on the resource allocation pattern (Müller & Steinger 1990; Müller 1990b). Nitrogen availability in the soil was found to influence greatly the compensatory responses to herbivory, highly increasing the negative effect of root herbivory to plants under nitrogen stress (Müller & Steinger 1990; Müller 1990b); nitrogen stress may well be caused by grass competition (see above).

Combined effects of intra- and interspecific competition

The fact that no significant interaction terms between knapweed density and grass competition were found for growth, biomass and fecundity suggests an additive effect of these two treatment factors. The effect of grass competition on survival, however, was found to be dependent on knapweed density, as the grass effect was more pronounced in the low density plots. This finding seems to contradict predictions of the cumulative stress model, assuming a higher competition pressure in the DG plots as compared to dG plots, as the grass effect, measured as above-ground biomass, was not found to be significantly different in low- and high-density plots. Nevertheless, interspecific competition may well be stronger than intraspecific competition due to increased root production of the grass in the low density plots. Hence, the combined effect of high density and grass competition did not further decrease plant height, survival and biomass production below the level achieved by grass competition alone (Fig. 3).

Response to herbivory as a function of the plant's competitive environment

Compensatory responses in plant height, survival, biomass and fecundity, as well as biomass production and seed output on the population level will be classified as overcompensation, equal compensation or undercompensation, depending on a significant positive, neutral, or negative effect of herbivory on these parameters (Belsky 1986). Variable plant responses to defoliation as a function of herbivore level (intrinsic factor) and the plant's competitive environment (extrinsic factors) have been found in a number of studies (Whittaker 1979; Lee & Bazzaz 1980; Berendse 1985; Cottam, Whittaker & Malloch 1986; Fowler & Rausher 1985; Paige & Whitham 1987; Maschinski & Whitham 1989; Louda, Keeler & Holt 1989). Similar interactions were also found in the very limited studies involving below-ground herbivores (mostly nematodes), but no studies have specifically addressed the consequences of removing below-ground storage tissue by herbivores on plant performance (Andersen 1987).

The compensatory response of *C. maculosa* varied greatly with the degree of density and grass competition (Fig. 3). In the absence of grass competition, herbivory showed no significant impact on plant height, biomass and fecundity. In association with grass as a single treatment factor, however, all plants had died in plots with intermediate levels of herbivory by March 1988. The combined effect of high density and grass competition on these parameters is complex, as both the effect of the combined treatment factors and of individual herbivory were generally less pronounced than in plots with grass competition alone, where no flowering plants survived. The above-mentioned possibility, that increased grass pressure in the low density plots leads to an overall reduced stress in the DG plots as compared to dG plots, is a possible explanation of these findings. Hence, these results indicate that the stress for plants growing in high density was below the 'threshold level' to equally compensate for herbivory, but above this critical stress level, where herbivory is detrimental, when growing in the more stressful grass neighbourhood.

The influence of the level of herbivory varied greatly for the different parameters measured. Surprisingly, a low level of herbivory significantly increased survival rate of *C. maculosa*, but the interpretation must be cautious because of the general low survival due to the clipping treatment. The significant linear negative relationship between herbivore density (log-transformed) and plant survival (Table 4) is in agreement with the cumulative stress model. The fact that only small and intermediate levels of herbivory decreased individual biomass and fecundity (Fig. 3c, d) may indicate that the few surviving plants in the DGH16 plots remained free from attack, whereas the plants in the other two herbivore treatments generally suffered from herbivory. This also explains the fact that only low and intermediate levels of infestation by *A. zoegana* increased the number of shoots (Fig. 3b). Increased shoot number is a consequence of the damage caused by the mining of early instar larvae to the apical meristem during the rosette stage of the plant. The removal of the apical dominance subsequently offsets the suppression of the dormant buds, allowing the growth of side shoots (Müller 1990b).

Consequently, none of the three herbivore levels reduced biomass production per area, as compared to the corresponding control plots (DGh). On a per-area basis, root herbivory reduced seed output by 20% on average, but this reduction was not significant due to high inter-plot variation.

Potential impact of A. zoegana *as a biological control agent*

Despite the knowledge gained from these experiments, realistic predictions of the outcome of the introduction of *A. zoegana* to control *C. maculosa* in North America remain difficult. Our findings, however, clearly demonstrate that the effect of root herbivores as biological control agents will mainly be determined by soil conditions and the competitive status of the weed. While the impact of seed feeders is generally limited to seed reduction, root herbivores can influence reproduction by (i) reducing the survivorship, (ii) delaying the time of flowering, and (iii) reducing seed output. The different life history of the targeted *C. maculosa* populations in North America (tetraploid, polycarpic, short-lived perennial) as compared to the studied *C. maculosa* plants (diploid, monocarpic, generally biennial) will further complicate predictions (Müller 1989a, 1989b). Preliminary studies carried out in British Columbia indicate that the population dynamics of *C. diffusa*, a closely related species, is little affected by reduced seed numbers, but that rosette survival is essential in determining knapweed equilibrium density, and that grass growth was greatly influenced by knapweed density (J. H. Myers, unpubl.). Recently started reseeding programmes to reduce knapweed density and to stabilize the density in the long term by refilling the empty niches once the knapweed population has declined, are most encouraging. Under the generally poor soil conditions of the infested areas, the main effect of the root herbivores on plant population dynamics will probably be through reduced rosette survival, as infested plants die relatively late in the growing season and will then be replaced by grass.

Biological control projects represent unique opportunities to test predictions of the outcome of herbivory on plant populations and community structure, and it is hoped that closer collaboration between biological control workers and plant population biologists will render biological weed control more predictive (Dirzo 1984; Müller 1990a; Schroeder *et al.* 1990).

ACKNOWLEDGMENTS

I thank E. Katz, R. Mühlemann, T. Steinger, S. Stinson, T. Köhler and M. del Mar for field assistance, B. Schmid for statistical advice and many helpful discussions. H. Rowell, B. Schmid, P. Klinkhamer, E. van der Meijden and two anonymous referees kindly commented on earlier drafts of this paper. Glasshouse space was provided by Ciba-Geigy. Paul Mäder, Research Institute for Organic Farming, Oberwil, helped in providing and managing the field plot. The research was supported by the 'Freiwillige Akademische Gesellschaft Basel' and the Swiss National Science Foundation.

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(*Received 14 June 1990; revision received 24 September 1990*)