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Seasonal changes in response of *Senecio ovatus* to grazing by the chrysomelid beetle *Chrysomela speciosissima*

Petr Pyšek

Institute of Applied Ecology, CS-28163 Kostelec n.Č.l., Czechoslovakia

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Summary. The response of *Senecio ovatus* to herbivory by *Chrysomela speciosissima* (Coleoptera, Chrysomelidae) was studied in the Krušné hory Mountains, Czechoslovakia. The following questions were addressed: (1) what is the impact of natural levels of insect herbivory on the performance of individual plants, (2) how do the levels of herbivory change during the growing period, and (3) what is the relative importance of direct and indirect effects of herbivory? Ten experimental plots sprayed with metathion and ten controls were established. Damage to plants was quantified in the period of maximum herbivore activity (June) and again at the end of the growing season (August). In the first half of the season, total leaf area in grazed ramets was reduced by 30.3% compared to ungrazed ramets; half of this reduction was due to beetle consumption and half was due to indirect effects. Individual leaf area was not significantly different between treatments. Insecticide-treated ramets were taller and heavier than the controls. During the second half of the growing period the differences in ramet weight and leaf area disappeared because of compensatory growth. However, the insecticide-treated ramets remained taller and had higher seed numbers per capitulum. Neither number of capitula per ramet nor seed weight were significantly different between treatments. In the grazed population, the leaf area reduction (30.3%) in June resulted in 36.5% reduction in fecundity at the end of August.

Key words: Herbivory – Direct and indirect effects – Compensatory growth – Leaf area losses – Fecundity reduction

There is a considerable body of literature demonstrating the effect of herbivory on plant performance (Harper 1977; Crawley 1983, 1988; Dirzo 1985; Edwards 1989). Especially over the last decade, many studies have concentrated on the way herbivory affects survival, growth and reproduction of plants (for reviews see Crawley 1983, 1988). Leaf damage by herbivores is common and well documented (e.g. Harper 1977; Robertson and Duke 1987; Landsberg 1989). Herbivory often modifies the growth of an individual plant and changes plant form either directly (by destroying meristems) and/or indirectly (by altering the pattern of resource allocation) (Crawley 1983, 1988; Waller 1986). The effects of herbivory on plant fitness are functions of the timing of damage with respect to the plant's developmental stage and of the quality and quantity of damaged tissue (Harper 1977; Dirzo 1984; Begon et al. 1986; Crawley 1988). Moreover, herbivores may have considerable impact on host plant population dynamics (Watkinson 1986; Crawley 1988), competitive interactions (Grace 1990; Louda et al. 1990) and the course of succession (Brown 1985; Gange et al. 1989).

Some individual plants can compensate for the effects of herbivory (Belsky 1986; Verkaar 1988) by altering physiological parameters during recovery (Prins et al. 1989). Whereas some authors have argued that herbivory may actually benefit a plant (Owen 1980; McNaughton 1983, 1986; Paige and Whitham 1987), surveys of the literature have led to a critical evaluation of these data (Verkaar 1988) concluding that there is, as yet, little convincing evidence supporting this contention (Belsky 1986, 1987). Some experimental studies (Cox and McEvoy 1983; Maschinski and Whitham 1989) show that interactions and responses are complicated.

In many studies herbivory has been simulated by artificial defoliation, or experiments have been performed in glasshouses, giving a high degree of precision at the expense of realism (Dirzo 1985). Such experiments may produce ambiguous results (Gange et al. 1989). On the other hand, in experiments attempting a higher degree of realism the results are often not so clear cut (Dirzo 1985). Herbivory may alter community structure and composition not only through direct effects on certain species but also indirectly through competition or interaction with the environment (Whittaker 1982; Parker and Salzman 1985; Gange et al. 1989; Louda et al. 1990). More field studies involving these latter aspects are thus needed.

This study addresses the following questions:

1. What is the impact of natural levels of insect herbivory on the performance of individual plants?
2. How do levels of herbivory change during the growing season?
3. Is it possible to estimate the relative importance of direct and indirect effects of herbivory?

Material and methods

Study site

The study site was located in the Krušné hory Mountains, Czechoslovakia, a crystalline mountain range (1244 m). The mean annual temperature is 5.0° C, precipitation 984 mm (50 year average). Experimental plots were located 1 km from the westernmost shore of the Fláje reservoir (district of Litvínov, Northern Bohemia, 50° 36′ N, 13° 17′ E) at an altitude of 840 m.

The study plots were located in areas deforested due to air pollution and covered by extensive stands of *Calamagrostis villosa* (Chaix) J.F. Gmelin, an invasive perennial grass (Pyšek 1990, 1991).

The plant species

Senecio ovatus (syn. *S. nemorensis* L. subsp. *fuchsii* (C.C. Gmelin) Čelak., *S. fuchsii* C.C. Gmelin) is a stout perennial forb 1.5–2 m in height, with lanceolate or elliptic-lanceolate leaves, 5–20 cm × 1–7 cm in size. The species is widely distributed in Central and Southern Europe (see Chater and Walters 1976 for details). It occurs in shaded habitats (both in original and secondary forests), along forest brooks, in clearings and damp meadows.

Senecio has a patchy distribution in the site studied. Its early emergence (April), through accumulated *Calamagrostis* litter, is followed by a period of fast growth, which makes the species capable of successfully competiting for light (Pyšek 1990).

Senecio is grazed by the polyphagous beetle, *Chrysomela speciosissima* Scopoli, which can cause considerable defoliation (Balachowski 1963). In 1990, feeding started in May, peaked at the end of June and finished by mid-July. *Chrysomela* was the only insect species feeding on plants of *Senecio* in the study area.

Sampling

At the beginning of the growing period (6 April 1990), ten experimental and ten control 2 × 2 m plots were established around *Senecio* plants. Ten randomly selected ramets were sampled from each plot and their height and dry weight were recorded in order to test for pre-treatment differences of plants.

Senecio occurring within the ten experimental plots was sprayed with metathion, a commercial insecticide containing 50 ± 2.5% of 0,0 dimethyl-0-(3 methyl 4 nitrophenyl) – thiophosphate. Control plots were sprayed with an equal volume of water. Spraying was carried out in the early morning or late afternoon to avoid hot, convective or windy weather conditions (Brown et al. 1987). The insecticide was applied with a hand-held sprayer. The amount of insecticide applied at each spraying was approximately 0.125 $\mathrm{l/m^{-2}}$. The spraying started in May and was repeated at 5–7 day intervals until chrysomelid feeding ended. The direct effects of the chemical on *Senecio* plants were not investigated since there were no undamaged control (insecticide-treated) plants present in the site which could have been compared with those undamaged because of insecticide application.

On 28 June 1990, after the period of maximum insect activity (visually estimated), ten randomly selected ramets were harvested from each plot. The following data were recorded for each ramet: height, basal diameter, number of branches (those shorter than 10 cm were not included), number of leaves, damage to stem tip. The area of each leaf for each plant was measured with LICOR LI-3100 area meter. Plant material was oven-dried at 80° C for 48 hrs and dry weights were determined separately for stems and leaves of all plants.

Leaf damage from herbivory was estimated by comparing the area of a damaged leaf to that of an undamaged leaf of the same length. Expected leaf area was predicted from leaf length using the regression between length and area based on measurements of 200 leaves collected from insecticide-treated (ungrazed) plants. These leaves represented the observed range of leaf lengths and widths. The leaf area was recorded as a mean of three area determinations with the area meter (Scott and Hastings 1987). In all leaves of grazed plants, the length of the midvein was recorded.

Also on 28 June 1990, another ten randomly selected ramets in each insecticide-treated and control plot were numbered with lastic tags and their height recorded. The extent of flowering in these ramets was assessed on 27 July, and on harvesting on 21 August 1990, vegetative characteristics were assessed in the same way as those sampled in June. In addition, at harvest time, numbers of capitula were recorded for each ramet, seed numbers were counted in 200 randomly selected capitula and the fresh weight of seeds was determined. Seeds were weighed in groups of ten ($n = 50$).

Results

Leaf area loss

At the June sampling, the total leaf area per *Senecio* ramet was 326.9 ± 16.5 $\mathrm{cm^{-2}}$ in ungrazed and 228.0 ± 12.3 $\mathrm{cm^{-2}}$ in grazed plots (Table 1). This difference was highly significant ($P < 0.001$). The observed reduction was due to both direct and indirect effects of herbivory.

The regression of leaf area on leaf length was: LEAF AREA = 0.2426 LEAF LENGTH$^{1.9021}$ ($P < 0.0001$, $r^2 = 0.87$). Total leaf area was obtained for each grazed ramet by summing the calculated areas of individual leaves. This value is considered as the potential leaf area of a ramet in the absence of herbivory. Hereafter it is referred to as "potential" leaf area in order to distinguish it from the value observed in the field. The difference between potential and observed values of the total leaf area of a ramet represents the leaf area loss.

In the control (grazed) plots, the potential leaf area was significantly lower than the observed leaf area recorded in insecticide-treated experimental plots ($F_{1,198} = 5.02$, $P < 0.05$). This reduction in leaf area (14.6%) may be considered as an indirect effect because grazed plants were smaller. In addition, there was significant decrease in the observed leaf area of grazed ramets in comparison with their potential leaf area ($F_{1,198} = 8.18$, $P < 0.05$). This difference (15.7%) represents the direct effect of herbivory due to leaf-feeding. If the total difference in the leaf area between insecticide-treated and grazed ramets (98.9 $\mathrm{cm^2}$ on average) is taken as 100%, the relative proportion of the indirect effect is 48.3% (47.8 $\mathrm{cm^2}$) and that of the direct effect 51.7% (51.1 $\mathrm{cm^2}$).

Table 1. Vegetative and reproductive characteristice of *Senecio ovatus* sampled from grazed and ungrazed plots at two harvesting dates

Number of ramets analysed	28 June			21 August		
	Grazed		Ungrazed	Grazed		Ungrazed
	100		100	73		68
Height (cm)	51.3 ± 1.4	***	62.8 ± 1.6	65.8 ± 2.0	***	80.7 ± 1.8
Basal diameter (mm)	5.7 ± 0.2	NS	5.4 ± 0.2	7.8 ± 0.3	***	6.2 ± 0.2
Weight (g) – total	4.1 ± 0.2	**	5.2 ± 0.3	7.9 ± 0.6	NS	8.2 ± 0.6
a) leaves	1.2 ± 0.1	***	1.6 ± 0.1	1.6 ± 0.1	NS	1.6 ± 0.1
b) stems	2.9 ± 0.2	*	3.6 ± 0.2	6.4 ± 0.5	NS	6.6 ± 0.5
Number of leaves	24.6 ± 1.1	*	29.2 ± 1.5	42.2 ± 2.9	*	32.1 ± 3.0
Individual leaf area (cm^2)	11.9 ± 0.4	NS	11.5 ± 0.4	5.1 ± 0.4	***	8.0 ± 0.4
Leaf area (cm^2) – total	228.0 ± 12.3	***	326.9 ± 16.5	231.0 ± 19.4	NS	238.7 ± 20.0
a) Branch leaves	49.7 ± 6.6					
b) Stem leaves	178.3 ± 9.0					
– Potential	279.1 ± 12.9					
– Estimated loss due grazing	51.1 ± 4.2					
– Relative loss (%)	20.6 ± 1.6					
Number of capitula/plant				49.7 ± 7.2	NS	61.5 ± 6.2
Number of seeds/capitulum ($n = 200$)				11.7 ± 0.2	***	14.9 ± 0.2
Weight of 10 seeds (mg) ($n = 50$)				8.3 ± 0.1	NS	8.4 ± 0.1

Means ± S.E. are given

Significant differences between treatments, as revealed by ANOVA, are indicated. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS non significant.

Number of ramets analysed in June and August differ, partly due to mortality and partly because some ramets were not relocated at harvest time.

Branch leaves were leaves produced in response to grazing and were not found on ungrazed ramets in June. In August, branch leaves and stem leaves were not analysed separately

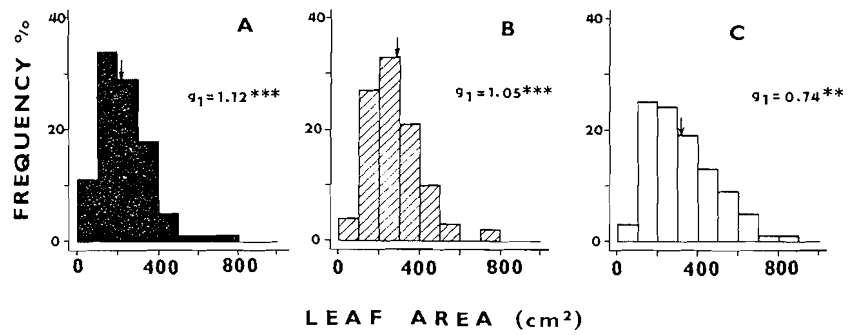

Fig. 1A–C. Frequency distributions of leaf areas: **A** observed values recorded for the grazed plants, **B** potential leaf area for grazed plants, **C** insecticide-treated plants. Means are indicated by *arrows* ($n = 100$, see Table 1 for values and SE). Values of skewness g_1 significantly different from 0 in two-tailed t-test are indicated: ** $P < 0.01$, *** $P < 0.001$

In plants influenced by herbivory, the frequency distribution of leaf area per ramet shows a shift towards the lower classes, being more skewed because of underrepresentation of ramets possessing large leaf areas (Fig. 1).

A significant correlation was found between leaf area loss and the potential leaf area in the grazed population ($P < 0.001$, $r = 0.39$) (Fig. 2A). This indicates that a higher amount of leaf tissue was removed from ramets possessing larger leaf area. The position of ramets with respect to the line of complete defoliation (Fig. 2A) shows that the probability of complete defoliation is higher in those ramets with the smallest leaf area, i.e. in the smallest ramets, as leaf area was positively correlated with ramet weight ($P < 0.01$, $r = 0.82$).

The relative damage to an individual ramet (expressed as percentage of tissue removed from the potential leaf area) decreases with increasing potential leaf area, i.e. with ramet size (Fig. 2B, $P < 0.001$, $r = -0.35$). Most plants do not suffer losses in leaf area greater than 40% (see frequency distribution of leaf area losses in Fig. 2A).

Effect of herbivory on vegetative characteristics

No significant differences in ramet height and weight were found at the beginning of the experiment (6 April).

The sampling carried out in late June revealed significant between-treatment differences in several vegetative characteristics (Table 1). In the insecticide-treated plots, plants grew taller and produced more leaves. Potential area of an individual leaf in the grazed population was not significantly different from the individual leaf area directly measured in the insecticide-treated plants. The significant difference between the total potential leaf area of grazed ramets and the total leaf area of ramets protected from grazing was thus mainly due to the reduction in leaf number for grazed plants.

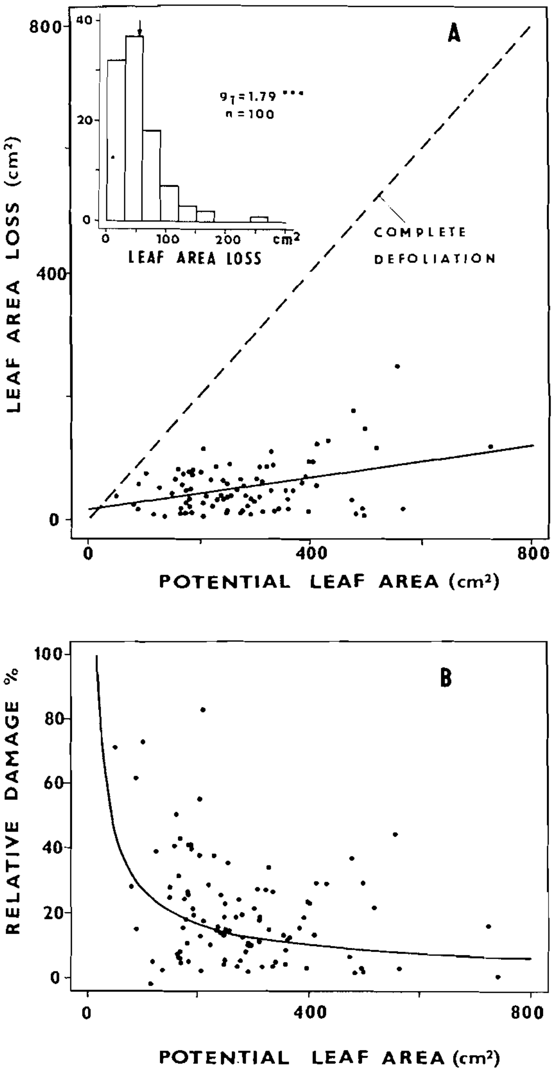

Fig. 2A, B. Relationship between potential leaf area of a ramet and **A** leaf area loss ($Y = 14.46 + 0.13X$, $r = 0.39$, $P < 0.01$, $n = 100$); **B** relative damage (percentage of the leaf area removed by leaf-feeding) ($Y = 0.298X^{-0.709}$, $r = -0.35$, $P < 0.001$, $n = 100$). Grazed population, data from 28 June 1991. Frequency distribution of leaf area losses due to direct grazing (i.e. the amount of leaf area directly removed by leaf-feeding) is shown in the top left part of **A**: mean is indicated by *arrow*, see Table 1 for the value and SE. Skewness g_1 was significantly different ($P < 0.001$) from 0 in two-tailed t-test

The reduction in weight as a result of herbivory was more conspicuous in leaves ($F_{1,198} = 10.35$, $P < 0.001$) than in stems ($F_{1,198} = 5.02$, $P < 0.01$).

At the end of the growing period, no significant differences in plant weight and total leaf area were found (Table 1). Nevertheless, differences were found: grazed ramets were shorter and had greater basal diameter. Furthermore, leaf number was higher in grazed ramets. This was in contrast to the June sample in which there were more leaves on ungrazed ramets. This difference was caused by the production of new leaves which developed on branches as a response to grazing. These branch leaves were smaller than the stem leaves and in August they were the main contributor to the leaf area of grazed ramets, whereas on the insecticide-treated

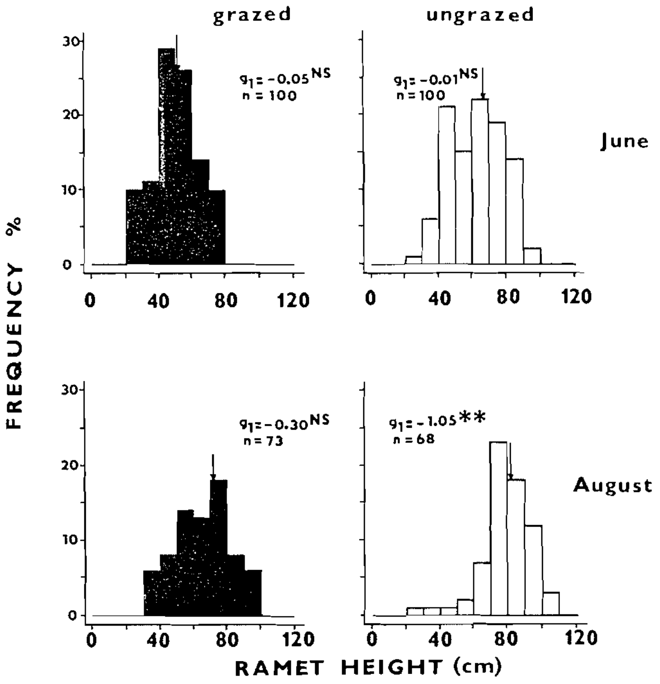

Fig. 3. Frequency distribution of ramet heights in grazed *(solid bars)* and insecticide-treated *(open bars)* plots in June and August. Means are indicated by *arrows* (see Table 1 for values and SE). Values of skewness g_1 significantly different from 0 in two-tailed t-test are indicated: ** $P < 0.01$, *NS* non-significant. Number of ramets analysed in June differs from that analysed in August, partly due to mortality and partly because some ramets were not relocated at harvest time

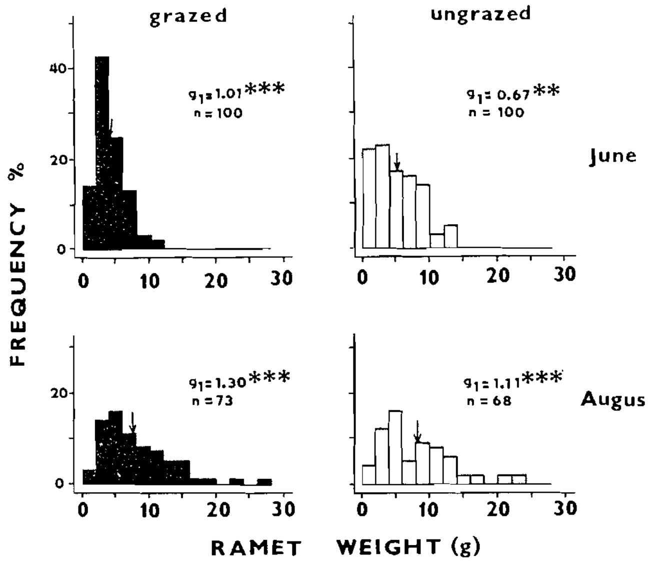

Fig. 4. Frequency distribution of total ramet weights in control *(solid bars)* and insecticide-treated *(open bars)* plots at two harvesting dates. Means are indicated by *arrows* (see Table 1 for values and SE). Values of skewness g_1 significantly different from 0 in two-tailed t-test are indicated: ** $P < 0.01$, *** $P < 0.001$. Number of ramets analysed in June differs from that analysed in August, partly due to mortality and partly because some ramets were not found at harvest time

Table 2. Differences in some morphological traits between grazed and insecticide-treated ramets

	28 June		21 August	
	Grazed	Ungrazed	Grazed	Ungrazed
Damaged stem tips (%)	49.0 ± 4.8 ***	5.0 ± 2.2	51.7 ± 7.1 **	15.7 ± 6.2
Proportion of branched ramets (%)	54.0 ± 4.5 ***	22.0 ± 3.2	85.1 ± 3.1 **	51.4 ± 7.7
Number of branched ramets analysed	54	23	61	36
Mean number of branches > 10 cm per branched ramet	3.6 ± 0.3 NS	4.8 ± 0.6	6.2 ± 0.5 NS	6.8 ± 1.1

Tip damage and branching was evaluated as a percentage of ramets in 2 × 2 m plots ($n = 10$). Number of branches represents the mean value per ramet. Means ± S.E. are given. Significant differences between treatments as revealed by Kruskall–Wallis test are indicated: ** $P < 0.01$, *** $P < 0.001$, NS non significant

ramets the large stem leaves were still present. The individual leaf area was thus still significantly higher in the insecticide-treated plots.

In late June, the frequency distribution of plant height in either treatment was not skewed (Fig. 3). However, in August, the ungrazed population had a negatively skewed height distribution ($g_1 = -1.05$, $P < 0.01$, two-tailed t-test), whereas the skewness of the height distribution in the grazed population ($g_1 = -0.30$) was not significantly different from 0. This suggests that the grazed population had the higher proportion of the shortest plants. The number of large plants was reduced by herbivory (Fig. 3).

The frequency distribution of total weight in June shows that the grazed population contained more ramets of medium size classes (Fig. 4). In August, similar frequency distributions were obtained in both grazed and insecticide-treated plots (Fig. 4).

Ramets affected by herbivory showed a higher percentage of damaged stem tips and were already more branched by the June sample (Table 2). This suggests that the regrowth of the grazed plants started before the late June sample, probably immediately after the intensive grazing had occurred.

Effect of herbivory on reproductive characteristics

Delay in flowering due to herbivory was recorded. On 27 July almost all insecticide-treated ramets were either flowering or in bud ($x \pm \mathrm{SE} = 99.0 \pm 1.0\%$, estimated as a mean percentage calculated for ten plots) , whereas only 63.9 ± 7.2% flowered in the grazed population. This difference was highly significant in the Kruskal-Wallis test ($H = 15.45$, $P < 0.0001$).

No significant differences in the number of capitula occurred between treatments at the end of the growing period (Table 1). However the frequency distribution of the number of capitula in the grazed population showed that there were more ramets with low numbers of capitula in the grazed population (Fig. 5). On the other hand, ramets with the highest numbers of capitula were found in the grazed population. This led to the higher value of the coefficient of variation (124.6 vs. 83.1%) in the population under herbivory.

Seed number per capitulum was significantly higher in the insecticide-treated ramets (Table 1). Of 200 capitula analysed in each treatment, many (23% in grazed plants and 13% in insecticide-treated) contained undeveloped seeds. The ramets that suffered herbivory showed more variability in the number of viable seeds per capitulum (coefficient of variation 23.9%) than did insecticide-treated plants (C.V. 13.3%). There was a positive skew in frequency distribution of number of seeds per capitulum ($g_1 = 0.59$, $P < 0.01$, two-tailed t-test) in the grazed population and a negatively (but non significantly,

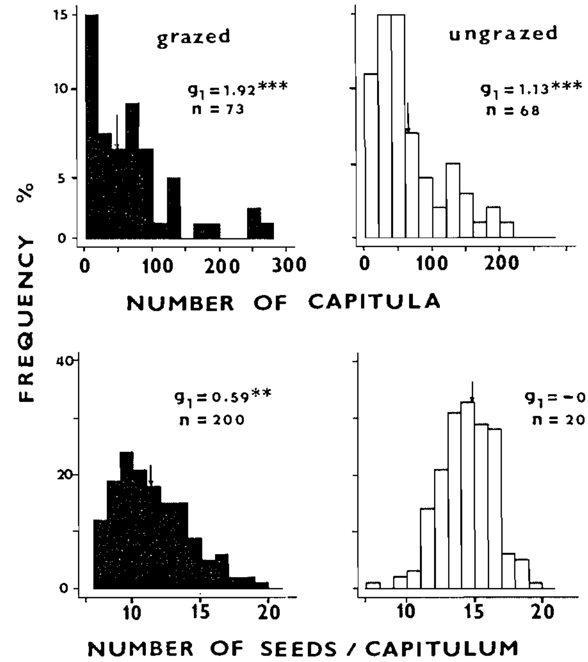

Fig. 5. Frequency distribution of the number of capitula per plant, and number of seeds per capitulum in the grazed *(solid bars)* and insecticide-treated populations *(open bars)*. Data from harvest, 21 August 1991. Mean values are indicated by *arrows* (see Table 1 for the values and SE). Values of skewness g_1 significantly different from 0 in two-tailed t-test are indicated: ** $P < 0.01$, *** $P < 0.001$, NS non significant

$g_1 = -0.23$) skewed frequency distribution of number of seeds per capitulum for the insecticide-treated one (Fig. 5).

Total number of seeds per ramet was 916.3 ± 92.4 (calculated for each ramet as a number of capitula multiplied by mean number of seeds per capitulum for a given treatment) in the insecticide-treated population and 581.3 ± 84.8 in the grazed population. The difference between treatments was significant ($F_{1,139} = 7.16$, $P < 0.01$). This represents a decrease of 36.5% due to herbivory. Average seed weight, however, was unaffected by treatment (Table 1).

Effect of herbivory on mortality

Of those plants labelled in June, 17.0 ± 5.4% died in the grazed plots and 8.0 ± 2.5% in the insecticide-treated plots; the difference between treatments was not significant (Kruskal-Wallis test). Within both treatments, plants which died were consistently and significantly shorter in late June than those that survived. A higher level of significance for the difference in height between the survivors and those ramets that died was found in the grazed plots ($F_{1,88} = 27.27$, $P < 0.001$) than in the insecticide-treated plots ($F_{1,74} = 4.79$, $P < 0.05$). However, the comparison of treatments is limited by the high proportion of plants not found during the late August sampling (10% in grazed and 24% in ungrazed plots).

Discussion

Herbivory can have a negative effect on the growth and reproduction of plants (Louda 1984; Belsky 1986; Verkaar 1988; Brown et al. 1988). In *Senecio ovatus* the reduction of leaf area (by 30.3%) and total weight (by 21.2%) recorded in the period of maximum herbivore activity (late June) resulted in a 36.5% reduction in seed number by the end of growing period (August). Some authors have reported increased leaf production as a result of herbivory (McNaughton 1983; Louda 1984). However, in one case, plants protected from herbivory increased total leaf area by adding leaves; the area of individual leaf was unchanged (Gange et al. 1989). Both increased and decreased leaf production may occur and may be revealed only if plants are examined over the whole growing season. In *Senecio,* more stem leaves were produced initially by the insecticide-treated plants, and these ramets grew taller than grazed ramets. Decrease in leaf area of grazed plants was thus partly due to lower leaf number. However, compensatory growth linked with the production of new branches in response to stem tip damage occurred on grazed plants in the second half of the growing period. The comparison of leaf area response in grazed and ungrazed populations may thus be dependent on the sampling time.

Herbivory may act on fecundity by changing (a) the number of inflorescences, (b) the number of seeds maturing per inflorescence, and (c) seed size. Various combinations of these effects have been reported (Bentley et al. 1980; Louda 1982, 1983; Speight and Whittaker 1982; Gange et al. 1989; Wisdom et al. 1989) and explained by the timing of herbivore attack (Harper 1977). The population dynamics may be affected when smaller seeds are produced as such seeds often fail to produce strong seedlings (Harper 1977; Gange et al. 1989). In *Senecio,* seed size was unaffected, but total fecundity was reduced in grazed plants. At the study site, *Senecio* occurs in a habitat where ground surface is mostly covered by a thick layer of accumulated grass *(Calamagrostis)* litter. Availability of safe sites (*sensu* Harper 1977) seems to be low in this habitat and the reduction of the seed number in plants suffering herbivory may thus act as a limiting factor to the spread of *Senecio* into deforested areas.

Pimentel (1988) argued that tissue removed from various plant hosts by herbivore populations averages about 7%. The value found in the present study (18.2% of the leaf directly removed by grazing) is twice Pimentel's average estimate. However, the percentage of leaf damage reported may reach 100% under natural levels of herbivory (Verkaar 1988).

The methodology employed for measuring and calculating defoliation can influence the values obtained. Moreover, these are often expressed as mean percentage defoliation without further information about its derivation (Landsberg 1989). The estimation of leaf area losses used in the present study was made possible by the pattern of leaf-feeding by *Chrysomela.* It is concentrated on the leaf blade leaving the midvein undamaged. The measurement of herbivory in this study was "instantaneous" (i.e. a single measurement); it was carried out at the time of maximum injury to plants' vegetative tissues. In general, some factors (e.g. dropping of heavily damaged leaves, leaf turnover rate) may lead to erroneous measurements and underestimation of herbivory. These factors were not considered in the present study, since leaf dehiscence was very rare in June.

Separation of the direct effect of herbivory (by a decrease in leaf area due to removal) from the indirect effect (by a decrease in leaf area due to herbivore-induced changes in plant structure, leaf phenology, and plant physiology) would be a significant advance in the analysis of the effects of insect herbivores on plant performance. The direct effect is suggested to have been satisfactorily quantified in this study. However, the indirect effects may be ascribed to differences in ramet size which can also include, apart from the indirect effect of herbivory, the arteficial impact of the insecticide on plant growth. Indeed, phytostimulation by insecticides on crop plants has been reported in several studies (see Brown et al. 1987 for references).

Size variability of plants suffering from natural insect herbivory has been reported to increase (Dirzo 1984; Gange et al. 1989). In *Senecio,* size variability expressed as the coefficient of variation was lower in the grazed population (54.7%) than in the insecticide-treated one (62.8%). Smaller plants were underrepresented and may have suffered increased herbivory-related mortality, whereas the potentially largest plants might have been reduced in size due to herbivory. More individuals were thus found in the middle size classes (Fig. 5). At the end of the growing period, the values of the coefficient of variation were almost equal (64.8% in grazed population vs. 63.4% in the insectide-treated one).

Conclusions

1. The natural level of herbivory by *Chrysomela* negatively affected the performance of *Senecio* plants. By the peak of herbivore activity (June), reduction in leaf area, weight and height was found in the grazed plants compared to those ungrazed. 2. Compensatory growth occurred during the second half of the growing period so that no significant differences in weight and leaf area were found at the end of August. In the grazed population, the leaf area reduction of 30.3% in June resulted in 36.5% reduction in fecundity at the end of August. Seed size was, however, not affected by grazing. 3. It was estimated that indirect effects of herbivory resulting from smaller ramet size accounted for 14.6% of the leaf area reduction and the remaining 15.7% was due to direct effects of leaf feeding. However, unambiguous separation of these effects was not possible because the insecticide treatment could have affected the growth of plants.

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References

Balachowski AS (1963) Entomologie appliquée a l'agriculturé. 1. Coleoptéres. Masson, Paris

Begon M, Harper JL, Townsend CR (1986) Ecology. Individuals, populations and communities. Blackwell, Oxford

Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. Am Nat 127:870–892

Belsky AJ (1987) The effects of grazing: Confounding of ecosystem, community, and organism scales. Am Nat 129:777–783

Bentley S, Whittaker JB, Malloch AJC (1980) Field experiment on the effect of grazing by a chrysomelid beetle *(Gastrophysa viridula)* on seed production and quality in *Rumex obtusifolius* and *R. crispus*. J Ecol 68:671–674

Brown VK (1985) Insect herbivores and plant succession. Oikos 44:17–22

Brown VK, Leijn M, Stinson CSA (1987) The experimental manipulation of insect herbivore load by the use of an insecticide (malathion): The effect of application on plant growth. Oecologia 72:377–381

Brown VK, Gange AC, Gibson CWD (1988) Insect herbivory and vegetational structure. In: Werger MJA et al. (eds) Plant form and vegetation structure. SPB Academic, The Hague, pp 263–279

Chater AO, Walters SM (1976) *Senecio*. In: Tutin TG, Heywood VH (eds.) Flora Europaea, Vol. 4. Cambridge Univ. Press, Cambridge, pp 191–205

Cox CS, McEvoy PB (1983) Effect of summer moisture stress on the capacity of tansy ragwort *(Senecio jacobaea)* to compensate for defoliation by cinnabar moth *(Tyria jacobeae)*. J Appl Ecol 20:225–234

Crawley MJ (1983) Herbivory: The dynamics of animal-plant interactions. Blackwell Scientific, Oxford

Crawley MJ (1988) Herbivores and plant population dynamics. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology. Blackwell Scientific, Oxford, pp 367–392

Dirzo R (1984) Herbivory: A phytocentric overview. In: Dirzo R, Sarukhán J (eds) Perspectives on plant population ecology. Sinauer, Sunderland, pp 141–165

Dirzo R (1985) The role of grazing animal. In: White J (ed.) Studies on plant demography. Academic Press, London, pp 343–355

Edwards PJ (1989) Insect herbivory and plant defence theory. In: Grubb PJ, Whittaker JB (eds) Towards a more exact ecology, Blackwell, Oxford, pp 275–297

Gange AC, Brown VK, Evans IM, Storr AL (1989) Variation in the impact of insect herbivory on *Trifolium pratense* through early plant succession. J Ecol 77:537–551

Grace JB (1990) On the relationship between plant traits and competitive ability. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 51–65

Harper JL (1977) Population biology of plants. Academic Press, London

Landsberg J (1988) A comparison of methods for assessing defoliation, tested on eucalypt trees. Aust J Ecol 14:423–440

Louda SM (1982) Distribution ecology. Variation in plant recruitment over a gradient in relation to insect seed predation. Ecol Monogr 52:25–41

Louda SM (1983) Seed predation and seedling mortality in the recruitment of the shrub *Haplopappus venetus* (Asteraceae), along a climatic gradient. Ecology 64:511–521

Louda SM (1984) Herbivore effect on stature, fruiting and leaf dynamics of a native crucifer. Ecology 65:1379–1386

Louda SM, Keeler KH, Holt RD (1990) Herbivore influences on plant performance and competitive interactions. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 414–444

Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: The influence of plant association, nutrient availability and timing. Am Nat 134:1–19

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336

McNaughton SJ (1986) On plants and herbivores. Am Nat 128:765–770

Owen DF (1980) How plants may benefit from the animals that eat them. Oikos 35:230–235

Paige KN, Whitham TG (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. Am Nat 129:407–416

Parker MA, Salzman AG (1985) Herbivore exclosure and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. J Ecol 73:903–913

Pimentel D (1988) Herbivore population feeding pressure on plant hosts: feedback evolution and host conservation. Oikos 53:289–302

Prins AH, Verkaar HJ, van den Herik A (1989) Responses of *Cynoglossum officinale* L. and *Senecio jacobaea* L. to various degrees of defoliation. New Phytol 111:725–731

Pyšek P (1990) The influence of *Calamagrostis villosa* on the species diversity of deforested sites in the Krusné hory Mts. Preslia 62:323–335

Pyšek P (1991) Biomass production and size structure of *Calamagrostis villosa* in different habitats. Preslia 63:7–18

Robertson AI, Duke NC (1987) Insect herbivory on mangrove leaves in North Queensland. Aust J Ecol 12:1–7

Scott ML, Haskins JL (1987) Effects of grazing by chrysomelid beetles on two wetland herbaceous species. Bull Torrey Bot Club 114:13–17

Speight RI, Whittaker JB (1987) Interactions between the chrysomelid beetle *Gastrophysa viridula*, the weed *Rumex obtusifolius* and the herbicide asulam. J Appl Ecol 24:119–12

Verkaar HJ (1988) Are defoliators beneficial for their host plants in terrestrial ecosystems – a review? Acta Bot Neerl 37:137–152

Waller DA (1986) The dynamics of growth and form. In: Crawley MJ (ed) Plant ecology. Blackwell, Oxford, pp 291–320

Watkinson AR (1986) Plant population dynamics. In: Crawley MJ (ed) Plant ecology. Blackwell, Oxford, pp 137–184

Whittaker JB (1982) The effect of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on growth and survival of *Rumex crispus* on a shingle bank. J Ecol 70:291–296

Wisdom CS, Crawford CS, Aldon EF (1989) Influence of insect herbivory on photosynthetic area and reproduction in *Gutierrezia* species. J Ecol 77:685–692