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Alejandro Morón-Ríos · Rodolfo Dirzo
Victor J. Jaramillo

Defoliation and below-ground herbivory in the grass *Muhlenbergia quadridentata*: Effects on plant performance and on the root-feeder *Phyllophaga* sp. (Coleoptera, Melolonthidae)

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Abstract In this study we evaluated (1) the combined effects of simulated defoliation and below-ground herbivory (BGH) on the biomass and nitrogen content of tillers and roots of the bunchgrass *Muhlenbergia quadridentata* and (2) the effect of defoliation on the survival of third-instar root-feeder larvae of *Phyllophaga* sp. The experiment was performed in a pine forest area at an altitude of 3200 m above sea level. The grass and the root-feeder species were native and dominant in the understory and in the macroarthropod root-feeder communities, respectively. Plants were established in pots in the field and were subjected to the following treatments in a factorial design: simulated defoliation (three levels) and BGH (with or without root-feeder larvae) with ten replicates per treatment. Plants were defoliated three times at 2-month intervals. The interaction between defoliation and root herbivory was significant for all components of plant biomass. In every case, light defoliation with BGH decreased live above-ground, root and total plant biomass, and the number of live tillers by more than 50% with respect to the same defoliation level without root-feeders. Plants apparently did not compensate for the carbon drain by root-feeders when a high proportion of older leaves were not removed by defoliation. Plants under heavy defoliation were not affected by the presence of root-feeders and showed a greater live/dead above-ground biomass ratio than lightly defoliated and control plants. Defoliation and BGH did not change tiller and root N concentrations but root herbivores did decrease live-tiller N content in lightly defoliated plants. Root-feeders but not defoliation decreased the root/shoot ratio by 40% and the live/dead above-ground biomass ratio by 45% through increased tiller mortality. Survivorship and final biomass of *Phyllophaga* sp. larvae were not affected by defoliation treatments during the 6-month study period.

Key words Grass · Defoliation · Below-ground herbivory · *Muhlenbergia quadridentata* · *Phyllophaga*

Introduction

Plant-herbivore studies have mostly concentrated on the consumption of foliage and stems, and on granivory (see Harper 1977; Brown et al. 1979; Crawley 1983; Price et al. 1991). Consumption of below-ground plant tissue has received, in contrast, little attention (Andersen 1987; Brown and Gange 1990). Furthermore, the joint effects of above- and below-ground herbivores and the consequences of root consumption on the growth and consumption of other plant parts have been poorly documented. Reichman and Smith (1991) reported that root biomass losses of 25% or 75% in *Tragopogon dubius* had a more severe effect on plant performance than a similar loss of foliage. In addition, root consumption reduced root biomass production, plant survival, and flower production. Ridsdill Smith (1977) found a reduction in both new root production and foliage growth following root consumption of *Lolium perenne*. This evidence suggests that root consumption may have comparable or even stronger effects than above-ground herbivory. Herbivory may increase plant nitrogen uptake and alter its allocation pattern (Ruess et al. 1983; Jaramillo and Detling 1988), which may allow plants to recover from grazing. In addition, carbon redistribution from roots to above-ground plant parts at moderate levels of herbivory may increase the root nitrogen concentration and tissue quality for root-feeders (Seastedt 1985; Seastedt et al. 1988). Thus, above-ground herb-

A. Morón-Ríos (✉)[1] · R. Dirzo · V. J. Jaramillo[2]
Centro de Ecología, UNAM, Ap. Post. 70-275, 04510 México, D.F., México

Present addresses:
[1]Ecosur, Depto. de Ecología y Sistemática Terrestre, A. P. 63 Sn, Cristóbal de las Casas 29290 Chiapas, México
e-mail: amoron@sclc.ecosur.mx; fax: (5) 967-8-23-22
[2]Centro de Ecología, UNAM, Unidad Regional Morelia, A.P. 27-3 Xangari 58089 Morelia, Mich. México

ivory, mediated by plant physiological responses, could have effects on below-ground herbivores. A conceptual model relating the two-way interaction between above- and below-ground insect herbivores has suggested that root herbivory may affect foliar feeders as well (Masters et al. 1993). Remarkably, with few exceptions (Moran and Whitham 1990; Masters and Brown 1992; Masters et al. 1993), this multiple interaction has not been frequently addressed.

The interaction between above- and below-ground herbivores has been studied at the community level but the sign and magnitude of the effects have been ambiguous (Hutchinson and King 1980; Roberts and Morton 1985; Seastedt et al. 1986). In some cases below-ground herbivore community biomass increased; in others it did not change. Single-species studies have shown an increase in above-ground herbivore biomass attributable to the activity of below-ground herbivores, but a decrease in root-feeder biomass and survival as a result of above-ground herbivory (Moran and Whitham 1990; Masters and Brown 1992).

Larvae of *Phyllophaga* are widespread below-ground herbivores which consume roots of wild plants, crops, ornamentals, orchards, and forest plantations, and decaying plant material as well (Morón 1986). Their life cycle lasts 1 year in tropical regimes, or up to 3 years in temperate areas. Oviposition occurs from late spring to early summer and eggs are laid near the host plant or in sites with high organic matter content. The species have three larval stages, of which the third is the longest (Ritcher 1957; Morón 1986). In México, the larvae of *Phyllophaga* are common in a variety of environments, including coniferous forests and subalpine grasslands.

Muhlenbergia quadridentata is a widespread species in the understory of pine and fir forests of México and has a regular to good forage value (COTECOCA 1995). These forests are frequently used for extensive cattle production and sustain a variety of herbivores (e.g., deer and rabbits). In the context of a larger project to evaluate the interaction between defoliation and below-ground herbivory (BGH) in a subalpine grassland (Morón-Ríos 1995), we set up an experiment to address the following questions. (a) What are the joint effects of defoliation and BGH on plant biomass and nitrogen content of tillers and roots of the grass *M. quadridentata*? (b) What is the effect of defoliation on the survival of third-instar root-feeder larvae of *Phyllophaga* sp.?

Materials and methods

Study area

The study site was located in the Zoquiapan Experimental Forest Station, 98°45′ W and 19°30′ N (División de Ciencias Forestales of the Universidad Autónoma Chapingo). The station lies within the Zoquiapan National Park in the neovolcanic belt of central Mexico at an altitude between 3000 and 3500 m (Franco and Búrquez 1981). Mean annual precipitation is 1169 mm and mean annual temperature is 11 °C (average of 20 years from Río Frío climatological station, located 8 km NNW of Zoquiapan). Precipitation occurs mostly between April and October with maxima in July and September. Maximum temperatures are registered in April and August and a frost period occurs between October and March.

The vegetation is a pine forest dominated by *Pinus hartwegii* Lindl. With the co-occurrence of *P. montezumae* Lamb., *P. leiophylla* Schl. & Cham., *P. ayacahuite* Ehr., *P. pseudostrobus* Lindl., *Abies religiosa* (H.B.K.) Cham. & Schl., *Cupressus lindleyi* Klotzsch., *Quercus crassipes* H. & B. *Q. rugosa* Née., *Q. laurina* H. & B. and *Alnus firmifolia* Fern. The understory is dominated by the grasses *M. quadridentata* (Kunth) Trin. and *Festuca tolucensis* H.B.K. which form a grassland-like plant community known locally as "zacatonal" (Obieta and Sarukhán 1981). These grasses are grazed by cattle all year round but there is no available information on the intensity and frequency of grazing. Deer and rabbits are the predominant natural grazers in the area, although their current densities are probably very diminished. Other grass species of the same genera are also present along with several herbaceous species.

Experimental protocol

Sixty individuals of *M. quadridentata* (23 ± 8 cm in height and 49 ± 24 tillers; mean ± SD) were collected in the study site in July 1993. Their roots were washed and fragments of wood and humus were discarded. Plants were grown individually in plastic pots 19 cm in diameter and 16 cm in height. Soil from the study site, previously sieved and mixed with sand in a 2:1 ratio, was used for the experiment to improve pot drainage and to make root recovery easier. Plants grew for 2 months prior to application of treatments.

In Septmeber 1993, 400 third-instar larvae of *Phyllophaga* sp. were collected at the same site. This instar is the longest (in temperate sites it extends for 14 months) and most voracious stage of the life cycle of this root-feeder (Morón 1986). Larvae were selected on the basis of their appearance and size. Individuals with necrotic spots or low mobility were discarded. Larvae were maintained for 1 week in pots with native soil to guarantee that they had not been damaged.

The experimental design was a completely randomized 3×2 factorial with artificial defoliation at three levels and BGH at two. Defoliation intensities were chosen as two extremes to explore their potential interaction with BGH: (1) control, without defoliation, (2) light defoliation, removal of 30% of the plant height, and (3) heavy defoliation, removal of 70% of the plant height. In the interpretation of this experiment, it is important to bear in mind that artificial defoliation or clipping treatments are less selective and removal of foliage may be more severe than actual grazing (Jameson 1963). In addition, artificial defoliation lacks the effects that animal trampling and urine deposition may have on the plant (Crawley 1983). BGH treatments were: (1) without larvae and (2) with ten *Phyllophaga* individuals per pot. Plants under field conditions can experience densities ranging from 0 to 25 larvae/plant because root-feeders have a highly aggregated pattern of distribution [see Morón-Ríos et al. (1997) for details on the spatial distribution and densities of *Phyllophaga* at this site]. The mean initial weight of the 30 groups of larvae (ten larvae/group) was 1.42 ± 0.002 g and there were no differences among the groups randomly assigned to experimental treatments ($F_{2,29} = 0.1619$, $P = 0.85$). Plants were defoliated to the same defoliation height every 2 months, at which time they had regrown more than 2 cm. Experimental units (pot with an individual plant) were randomly assigned to treatments with ten replicates each. The experiment was carried out at the Forest Station within a fenced area from October 1993 to June 1994. Thus, plants were defoliated three times during the experiment. Above-ground insect herbivores were generally absent in the experimental plot during the study period.

A pilot trial showed that pots placed on the soil surface had higher larval mortality than pots located in excavated pits (A. Morón-Ríos, unpublished data). Thus, experimental pots were placed in soil pits 19 cm in diameter and 10 cm deep to provide larvae with microclimatic conditions similar to their natural environment. Pots were randomly reallocated monthly and plants were watered as needed. Tiller number per plant was determined at the start of the experiment. Tillers cut at each defoliation were kept in paper bags. At harvest, dead and live tillers were counted. Roots were detached from the crown and carefully washed to remove soil. Care was taken to recover fine roots. All plant material was dried at 70 °C until weights stabilized. Larvae were counted and carefully washed to eliminate soil adhering to their body. They were dried with paper towels, weighed fresh, and fixed with Pampel solution. Total nitrogen concentration of roots and live tillers was determined with a micro-Kjeldahl procedure (Nelson and Sommers 1980). Above-ground plant production was determined by adding the weight of harvested material at each defoliation to that at final harvest.

Statistical analyses

Data analysis was performed with a two-way ANOVA and type III sum of squares (Shaw and Mitchell-Olds 1993) because of the uneven loss of replicates in some treatments due to vandalism. Sample size for each treatment is indicated in Fig. 1. Variables were square root transformed to satisfy homogeneity of variances and normality criteria when residual analysis of non-transformed data did not fulfil them. The Tukey-Kramer test for unbalanced data and unplanned comparisons was applied when the ANOVA showed significant ($P < 0.05$) treatment effects (Day and Quinn 1989). Survivorship (final number of individuals) and biomass of root-feeders were evaluated with a one-way ANOVA for unbalanced data (Lindman 1992). All data are presented in their original scale of measurement.

Results and discussion

The interaction of defoliation and BGH was significant for all components of biomass production (Table 1). In every case, light defoliation with BGH decreased live above-ground (Fig. 1A), root (Fig. 1B), and total plant biomass (Fig. 1C), and the number of live tillers (Fig. 2) by more than 50%, with respect to the same defoliation level without root-feeders. Root herbivory can decrease above-ground plant biomass and production (Ridsdill Smith 1977; Ladd and Buriff 1979; Ingham and Detling 1986; Gange and Brown 1989) and in our study this was particularly evident when plants experienced a light defoliation regime. The unexpected strong interaction between root herbivory and the light defoliation level could be attributed to the fact that the loss of 30% of

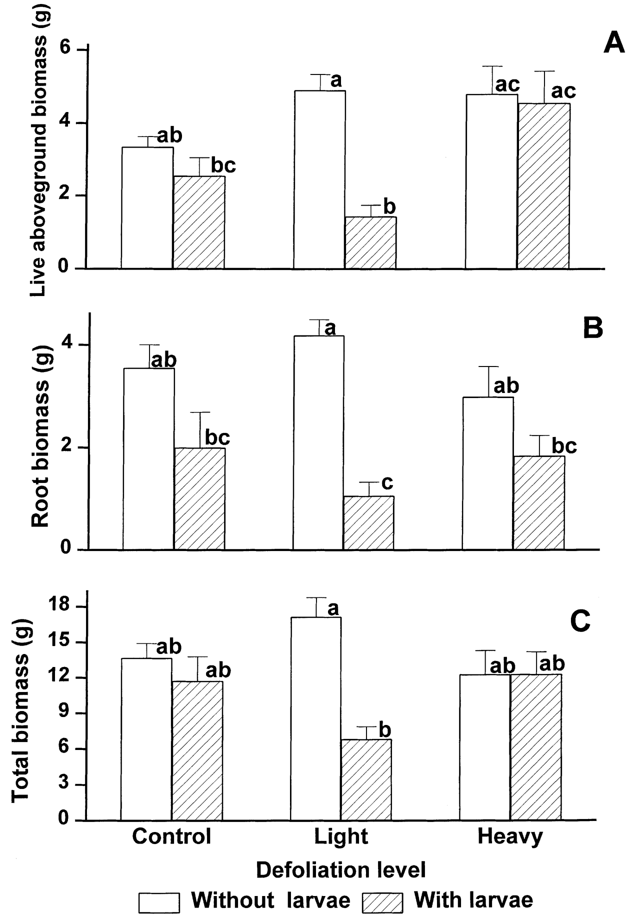

Fig. 1 Above-ground (**A**), root (**B**), and total (**C**) biomass of *Muhlenbergia* in response to above- and below-ground herbivory. Values are means of different numbers of replicates (+ 1 SD). Sample sizes were: $n = 6$ (control without larvae), $n = 8$ (control with larvae), $n = 9$ (light defoliation with and without larvae, heavy defoliation without larvae), $n = 7$ (heavy defoliation with larvae). *Bars* with different *letters* show significant differences ($P < 0.05$)

Table 1 ANOVA results for biomass and nitrogen variables in *Muhlenbergia quadridentata*. Sample size for each treatment is indicated in Fig. 1

Variable	BGH		Defoliation (D)		Interaction (BGH × D)	
	$F_{1,42}$	P	$F_{2,42}$	P	$F_{2,42}$	P
Above-ground live biomass	14.15	0.001	5.58	0.007	6.54	0.003
Above-ground total biomass	3.97	0.053	0.12	0.88	6.10	0.005
Root biomass	28.57	0.0001	0.25	0.78	3.26	0.048
Total biomass	8.27	0.006	0.08	0.92	5.37	0.008
Number of live tillers	2.68	0.109	1.69	0.19	4.48	0.017
Number of dead tillers	5.44	0.025	2.86	0.068	0.48	0.621
Root/shoot ratio	24.75	0.0001	1.19	0.315	1.65	0.204
Above-ground live/dead	15.19	0.0001	25.04	0.0001	0.82	0.45
%N live tillers	0.61	0.439	1.38	0.263	1.36	0.267
N content live tillers	11.58	0.001	1.23	0.302	6.68	0.003
% N root	0.20	0.659	1.34	0.272	0.45	0.639
N content root	33.81	0.0001	0.27	0.767	2.53	0.091

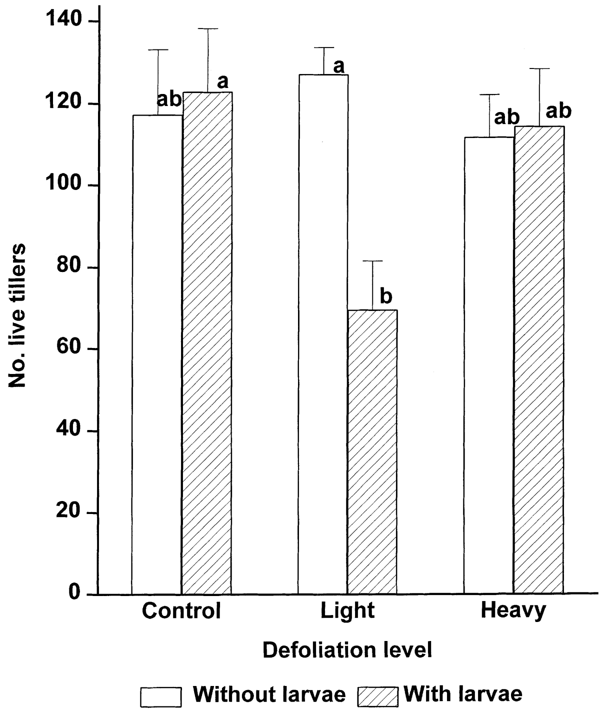

Fig. 2 Number of live tillers of *Muhlenbergia* in response to defoliation and below-ground herbivory. Values are means (+ 1 SD). Sample size for treatments as in Fig. 1. *Bars* with different *letters* show significant differences ($P < 0.05$)

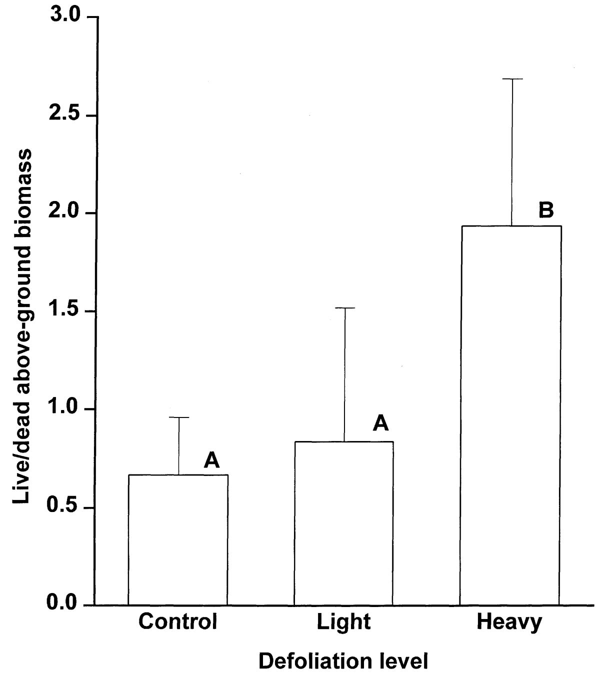

Fig. 3 Live/dead above-ground biomass ratio of *Muhlenbergia* in response to defoliation and below-ground herbivory. Values are means of different number of replicates (+ 1 SD). Sample sizes: $n = 14$ (control), $n = 18$ (light defoliation), $n = 16$ (heavy defoliation). *Bars* with different *letters* show significant differences ($P < 0.05$)

plant height did not remove a high proportion of old leaves, which show lower photosynthetic capacities than younger ones (Caldwell 1984) and predominate in the lower section of the plant (Langer 1979). Since carbohydrates for regrowth come initially more from photosynthesis than from storage (Richards and Caldwell 1985), carbon fixation by regrowth and older tissue apparently did not compensate for the carbon drain by root-feeders. Without root herbivores, plants were not detrimentally affected by light defoliation, and compensated (Belsky 1986) for lost tissue.

In contrast, heavily defoliated plants were not as affected by the presence of root-feeders (Fig. 1). They also showed a greater ($P < 0.001$) live/dead above-ground biomass ratio than lightly defoliated and control plants (Table 1, Fig. 3). Removal of 70% of the plant height may have resulted in these plants having more young, regrowth leaves, with greater photosynthetic capacities (Caldwell 1984) and less self-shading than plants subjected to the other defoliation treatment. These conditions should increase available carbon for above- and below-ground production, compensating for biomass lost to root-feeders.

Defoliation and BGH did not change the root N concentration (0.7 ± 0.2% N; Table 1), and did not affect root N content (Table 1). This does not support the hypothesis that defoliation may increase root nitrogen content due to both greater root mortality and greater microbial colonization of senescing roots (Seastedt et al. 1988). Moreover, neither defoliation nor BGH affected

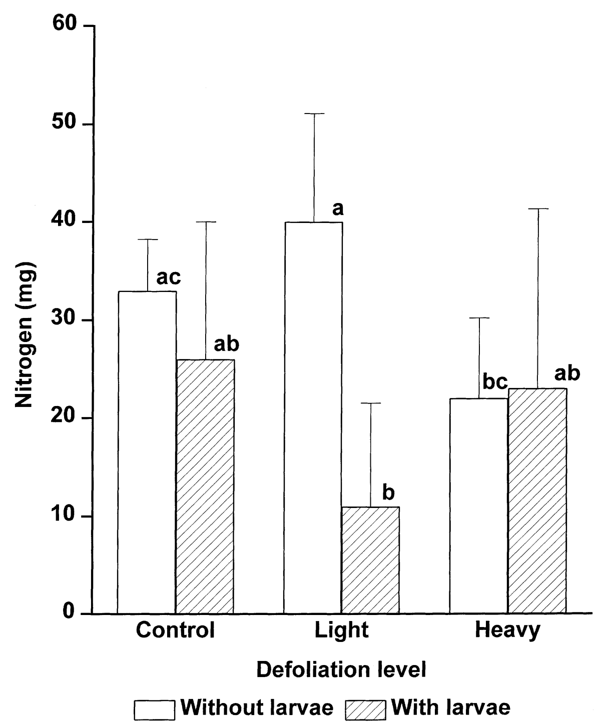

Fig. 4 Nitrogen content of live tillers of *Muhlenbergia* in response to defoliation and below-ground herbivory. Values are means (+ 1 SD). Sample size for treatments as in Fig. 1. *Bars* with different *letters* show significant differences ($P < 0.05$)

Table 2 Effects of below-ground herbivory on *M. quadridentata* for variables in which treatment interactions were not significant. Values are means (± 1 SD; $n = 24$). In all cases $P < 0.02$

Below-ground herbivory	Above-ground biomass live/dead	Root/shoot ratio	Dead tillers (n)	Root nitrogen content (mg)
Absent	1.5	0.37	72	25
	(0.91)	(0.12)	(36)	(9)
Present	0.81	0.22	94	11.2
	(0.56)	(0.11)	(30)	(8)

Table 3 Survivorship and biomass (mean ± 1 SD) of *Phyllophaga* sp. in response to defoliation treatments

Defoliation treatment	Survivorship mean ($F_{2,21} = 0.96, P = 0.4$)		Biomass mean ($F_{2,21} = 0.78, P = 0.47$)	
Control ($n = 8$)	5.25	(2.54)	0.539	(0.328)
Light defoliation ($n = 9$)	4	(1.93)	0.453	(0.189)
Heavy defoliation ($n = 7$)	5.28	(1.97)	0.606	(0.195)

tiller N concentration, and root herbivores decreased the live-tiller N content of lightly defoliated plants compared to both plants with the same defoliation level without BGH and control plants (no defoliation, no root feeders; Fig. 4). These results differ from those reported for *Capsella bursa-pastoris*, in which BGH increased foliar N content and concentration (Gange and Brown 1989). In our study, the possible carbon limitation imposed by root-feeders together with a light defoliation regime (see above) likely decreased the capacity of the plant to explore the soil environment and take up N. These defoliation and root herbivory effects are not in accordance with the arguments of Masters et al. (1993). In short, our perennial test species responded to defoliation in a manner similar to their proposal for annual plant behavior, and BGH did not increase the quality of above-ground tissues.

BGH but not defoliation significantly altered biomass allocation between roots and tillers (Tables 1, 2). Plants that grow under high grazing pressure generally increase biomass allocation to above-ground structures at the expense of roots, which allows them to recover from repeated defoliation (Caldwell et al. 1981; Detling and Painter 1983; Jaramillo and Detling 1988; Polley and Detling 1988; Painter et al. 1993). Our results suggest that *Muhlenbergia* did not have the plasticity to change its allocation pattern, although it did replace biomass lost by defoliation. It is possible that the defoliation frequency imposed did not push *Muhlenbergia* over the threshold beyond which it loses capacity to replace lost tissue (McNaughton 1983).

Some studies have shown that above-ground herbivory may decrease the population density or individual growth rate of below-ground herbivores (Moran and Whitham 1990; Masters and Brown 1992). Our results showed, in contrast, that survivorship and biomass of *Phyllophaga* sp. larvae were not affected by simulated defoliation after a 6-month period (Table 3). Larvae did not experience changes in food quality because defoliation did not significantly reduce the N concentration (Table 1). Food quantity (i.e., root biomass) decreased under light defoliation in the presence of larvae (Table 1, Fig. 1B) and could reduce larval survival and biomass. However, given that third-instar larvae can live for up to 14 months, a longer experiment would be required to evaluate this possibility.

Root-feeders decreased the live/dead above-ground biomass ratio by 45% because they increased tiller mortality (Table 2). This suggests that the activity of below-ground herbivores may affect resource availability for above-ground herbivores. Our results, like those reported for North American grasslands (Scott et al. 1979; Ingham and Detling 1986), also show that BGH can have more severe effects on plant performance than its above-ground counterpart. Under the experimental conditions of this study, root-feeders had a more severe impact than removal of up to 70% of the plant height. Together, these and other studies highlight the importance of root-feeders in herbivory research (Andersen 1987; Brown and Gange 1990), which usually includes only the above-ground component.

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