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BEETLE FOLIVORY INCREASES RESOURCE AVAILABILITY AND ALTERS PLANT INVASION IN MONOCULTURES OF GOLDENROD¹

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Abstract. One way that insect herbivores can influence plant community structure is by altering the ambient availability of resources required by plants. To examine the importance of this mechanism, I tested the following three hypotheses in a field experiment in 1990: (H_1) Folivory by the leaf beetle *Trirhabda canadensis* (Coleoptera: Chrysomelidae) increases availability of light, water, and N in monocultures of goldenrod (*Solidago missouriensis*). This hypothesis was partially supported. Folivory by *Trirhabda* reduced leaf, root, and total biomass of goldenrod and increased light penetration, soil water content, and soil nitrate concentration. However, *Trirhabda* grazing did not affect overall soil N availability. (H_2) The invasion of goldenrod monocultures by other plant species and the response of goldenrod to folivory reflects an increased availability of resources in monocultures grazed by *Trirhabda*. This hypothesis was supported. Folivory by *Trirhabda* raised the probability that a species would invade the experimental monocultures and increased the species richness of the invading plant assemblage. Relative growth rate of goldenrod and production of aboveground biomass by invaders were higher in monocultures grazed by *Trirhabda* than in ungrazed ones. Prostrate and creeping forbs increased in relative abundance following folivory by *Trirhabda*. (H_3) Reduced N uptake by goldenrod or increased N mineralization accompanies increased N availability in grazed monocultures. This hypothesis was also supported. Net N mineralization and nitrification were higher in monocultures grazed by *Trirhabda* than in ungrazed monocultures. Folivory by *Trirhabda* larvae reduced N uptake by goldenrod, but that of adults did not. The impact of herbivores upon plant communities may be effected through increased availability of important plant resources.

Key words: Cedar Creek Natural History Area, Minnesota; herbivory; invasion; light; nitrogen; resource availability; *Solidago*; *Trirhabda*; water.

INTRODUCTION

Herbivores can affect the productivity and species composition of terrestrial plant communities (Darwin 1859, Summerhayes 1941, Watt 1957, Ellison 1960, McNaughton 1984, Huntly 1991, Levin 1993). A common interpretation for these observations is that differential herbivory alters competitive relationships among the community's component species. Differential consumption, especially if it affects a dominant species, can permit other species in the community to increase in biomass or relative abundance. In addition, differential consumption can facilitate invasion of new species (Harper 1977, Connell 1978, Belsky 1986, Louda et al. 1990). An important mechanism is implicit within this phenomenological (*sensu* Tilman 1987a) explanation: herbivory might effect such changes by increasing the ambient availability of limiting resources (Tilman 1982, 1988, Inouye et al. 1987a, Huntly

and Inouye 1988, Huntly 1991). Consumers can increase available resource levels in intertidal communities (Connell 1961, Paine 1966, Lubchenco 1978, Lubchenco and Cubitt 1980), coral reefs (Carpenter 1986), freshwater hard-substratum communities (Power et al. 1988), and planktonic communities (Martin 1965, Lehman 1980, Sterner 1986, 1990). Since the availability of light and nutrients greatly influences the growth and interspecific interaction of terrestrial plants (Grime 1977, Harper 1977, Tilman 1988), altered resource availability may be a mechanism underlying competitive release following herbivory.

Population densities of phytophagous insects are often variable and can erupt under certain environmental conditions (Barbosa and Schultz 1987, Crawley 1989). These insect outbreaks can affect plant productivity and community structure by perturbing the rate of nutrient cycling (Chew 1974, Mattson and Addy 1975, Kitchell et al. 1979, Holland et al. 1992), but few studies have quantified how intense insect folivory affects resource availability or nutrient cycling (Swank et al. 1981, Ohmart et al. 1983, Lamb 1985, Waring and Pitman 1985, Hollinger 1986, Romme et al. 1986, Schowalter et al. 1986, Swank 1988, Veblen et al. 1991).

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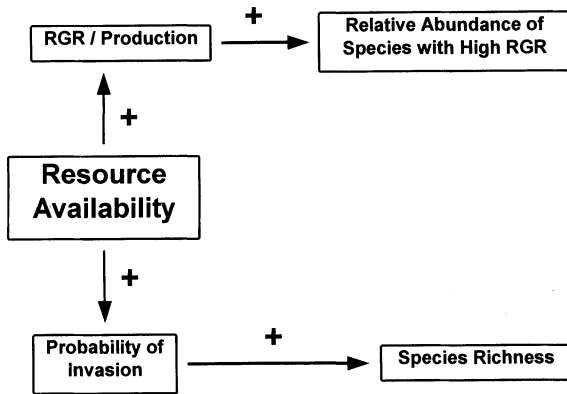


FIG. 1. Predicted responses of a plant community to an increase in resource availability. Elevated resource levels will augment the relative growth rate (RGR) or production of the plants in the community, and the relative abundance of rapidly growing species will increase. In addition, elevated resource availability will raise the probability that a given species can invade the community and concomitantly increase the species richness of the invading plant assemblage.

Chrysomelid beetles of the genus *Trirhabda* are important folivores of goldenrods (*Solidago* spp.) (Reid and Harmsen 1974, Messina and Root 1980, Messina 1981, McBrien et al. 1983, Root and Cappuccino 1992). Their extensive defoliation during outbreaks greatly reduces goldenrod biomass and alters the relative abundance of plant species in old-field communities dominated by goldenrods (Messina 1981, McBrien et al. 1983, Cain et al. 1991; D. G. Brown, *personal observation*). I used the *Solidago*–*Trirhabda* system to test the hypothesis that intense insect folivory increases the availability of light, water, and nitrogen in goldenrod monocultures. I then determined whether grazed monocultures and the plant assemblage that invaded them conformed with patterns predicted to accompany an increase in resource availability (Fig. 1): (a) Folivory increases the probability that a species will invade a monoculture, therefore grazed monocultures will support a more species-rich assemblage of invaders (Grubb 1977). (b) The relative growth rate of remaining goldenrod and biomass production by invaders will be higher in monocultures grazed by *Trirhabda*. (c) Species with characteristics associated with rapid relative growth rate will increase in relative abundance in grazed monocultures (Tilman 1988). I also tested the prediction that folivory by *Trirhabda* would increase N mineralization (Fig. 2; Detling 1988, Holland et al. 1992) or reduce N uptake by goldenrod (Fig. 2; Ruess 1988, Tilman 1988).

METHODS

Study site

I conducted this research at the Cedar Creek Natural History Area (CCNHA), which straddles the border of Anoka and Isanti counties in east-central Minnesota,

≈60 km north of Minneapolis/St. Paul. The general characteristics of CCNHA and its soils are described elsewhere (Grigal et al. 1974, Inouye et al. 1987b). Availability of soil nitrogen is a dominant factor influencing the growth and interspecific competition of plants at CCNHA (Tilman 1984, 1987b). The study site was an old field abandoned from soybean production in 1961. Its soil was a well-drained uniform outwash sand with low total N content (≈500 mg/kg soil) and low organic matter content (<1% by mass). Grasses are the dominant vegetation type in the field; *Poa pratensis*, *Agropyron repens*, *Setaria glauca*, and *Panicum* spp. were the most common species. Common forbs were *Ambrosia artemisiifolia*, *Berteroa incana*, *Erigeron* spp., *Vicia villosa*, and *Physalis* spp. Dense patches of mosses and soil lichens were among the forbs and grasses.

Study species

Solidago missouriensis (Nutt) (Missouri goldenrod) is a short rhizomatous perennial herb (20–40 cm tall in CCNHA old fields) typically found in dry, infertile sites (Werner 1976). It occurs in discrete clones throughout CCNHA, generally in fields of mid-successional age (20–30 yr) through undisturbed oak savanna habitat. *S. missouriensis* is one of several goldenrods consumed by both the larvae and adults of *Trirhabda canadensis* (Kirby) (Coleoptera: Chrysomelidae). Baldur (1929) details the life history of *T. canadensis*. At CCNHA, eggs oviposited in the soil or litter beneath a goldenrod clone during the previous summer hatch in early through mid-May. Larvae feed for ≈1 mo and subsequently pupate in the soil under their host clone. Adults emerge in late June–early July and simultaneously feed and mate on goldenrods through July and into August. Populations of *T. canadensis* erupt asynchronously on clones of *S. missouriensis*, *S. altissima*, and *S. gigantea* at CCNHA. During these eruptions *T. canadensis* can consume all leaf tis-

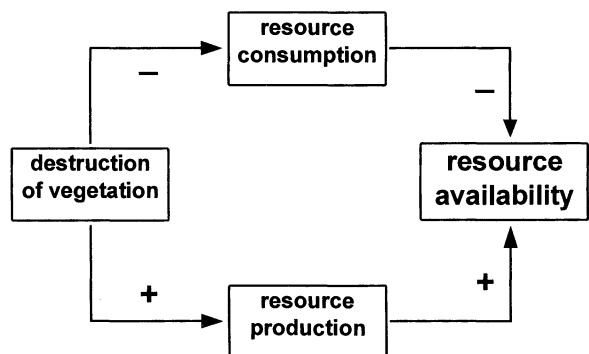


FIG. 2. Paths by which herbivory can alter resource availability. Resource consumption by plants reduces resource availability. Herbivory, by reducing the density of resource-harvesting plant biomass will therefore have a net positive effect upon resource availability. Herbivory may also stimulate resource production (e.g., N mineralization), which will also increase resource availability.

sue in their host clone (D. G. Brown, *personal observation*). Larvae of *T. canadensis* generally do not leave a goldenrod clone unless all of its leaf material has been consumed. The adults are also relatively sedentary (Messina 1982; D. G. Brown, *personal observation*), but will emigrate if there is a local shortage of food or potential mates (Morrow et al. 1989).

Experimental setup

I prepared 36 circular plots 1 m in diameter (0.785 m²) during the summer of 1987. I arrayed them in three discrete blocks consisting of three rows of four plots each; adjacent plots in the same row or column were 7 m apart. I surrounded each plot with aluminum flashing sunk to a depth of 20 cm, which was approximately the maximum rooting depth of *S. missouriensis* at CCNHA (D. G. Brown, *personal observation*). No *S. missouriensis* ramets emerged outside the plots during the experiment. I sprayed each plot several times with Roundup (Monsanto), a broad-spectrum herbicide, to remove all living vegetation before the experiment. Soil microbes rapidly metabolize Roundup and subsequent effects are negligible.

I collected small clumps of 3–5 *S. missouriensis* ramets in June 1987 by excavating cubes of soil 20 cm on a side from a large clone that I had demonstrated in preference tests to be acceptable food for adult *T. canadensis*. I placed these ramet clumps into 2-L pots filled with a 9:1 mixture of sifted CCNHA topsoil and peat moss and watered them every other day until late August. I then selected the most robust and randomly transplanted them into the experimental plots. I initially assigned plots within each block randomly to one of three folivory treatments: none, low (1 *Trirhabda*/ramet), or high (5 *Trirhabda*/ramet). These densities were lower than those that can occur at the zenith of a *Trirhabda* outbreak (D. G. Brown, *personal observation*). I did this so that *Trirhabda* would not destroy the goldenrod monocultures in a single season. Low and high folivory treatments had similar responses for the factors considered in this study; I therefore pooled them into a single *Trirhabda* addition treatment [*Tri*(+), $N = 24$] to simplify data analysis. I contrasted this composite treatment with the no-folivory treatment [*Trirhabda* removal or *Tri*(–), $N = 12$]. In May of 1988 I assessed plant growth in the experimental plots and transplanted additional ramets into those where the density was not sufficient. *Tri*(+) and *Tri*(–) monocultures did not initially differ in their mean height or number of ramets ($t < 0.6$, $df = 30$, $P > 0.5$). I watered plots weekly between late May and mid-August of 1988 and from mid-May to mid-June of 1989. Goldenrod monocultures were then well established and received no further water augmentation.

In July 1989 I used beetles collected from colonies maintained by P. A. Morrow and G. M. Puttick to stock *Tri*(+) plots. I used no enclosures, but maintained adult densities by regular censuses and appro-

priate removal, transfer, or restocking. I did not attempt to control larval densities in *Tri*(+) plots in 1990. A census in late May, when larvae were entering their third instar, showed that these plots averaged 4.12 ± 0.44 larvae/ramet (mean ± 1 SE). I sprayed *Tri*(–) plots with Insecticidal Soap (Safer, Ringer Company, Eden Prairie, Minnesota, USA) in early May 1990 while larvae were in their first instar. I subsequently removed as many surviving larvae as possible from them to minimize leaf damage. Despite my efforts *Tri*(–) plots averaged 0.75 ± 0.25 larvae/ramet. I maintained adult densities through July and August of 1990 as described above.

Since other folivores of *S. missouriensis* at CCNHA were extremely rare, I made no attempt to exclude them. Many predators find *T. canadensis* distasteful (P. A. Morrow, *personal communication*). Predaceous sucking insects and spiders will consume *T. canadensis*, so I removed them from experimental plots when their abundance was high. Pocket gophers (*Geomys bursarius*) are very common at CCNHA. I attempted to trap them before they entered the experimental blocks, but made no other attempt to exclude them. Gophers invaded one-third of the experimental plots during the experiment. I attempted to remove any effects of gopher damage by treating it as a covariate during statistical analysis.

Leaf damage and growth of *S. missouriensis*

I assessed leaf damage in experimental monocultures in 1990 after larval pupation (June) and after adult *Trirhabda* perished (August). Leaves sampled for damage in August were produced after larval feeding; larval damage was not counted twice. I systematically selected 12 ramets on three regularly spaced transects across each plot and visually assessed the percentage of leaf area missing from each fully expanded, non-senescent leaf on the selected ramets using a 12-point scale (undamaged; >0 – $<10\%$ leaf area consumed, 10 – $<20\%$, 20 – $<30\%$, etc; 100% consumed). In addition, I took a subsample of leaves, reconstructed their undamaged form by eye, and determined leaf area loss by digitization. Leaf area loss estimates obtained by these two methods corresponded well ($r^2 = 0.976$, slope of regression line not significantly different from 1.0).

I estimated goldenrod biomass in the experimental monocultures in June 1990 (after larval feeding) and in September of 1989 and 1990 (after adult feeding). I collected aboveground biomass by clipping a 10×50 cm strip that was located in the same position in each plot. I took four 5 cm diameter \times 40 cm deep soil cores within the clipped area to collect roots and rhizomes. I refilled holes with soil from nearby pocket gopher mounds and marked the clipped area to prevent resampling. I washed soil from the cores through a 1-mm mesh screen and separated living roots and rhizomes from the remaining organic bolus by floating it in water and removing the roots and rhizomes with

forceps. I sorted the plant material into different functional components, dried it at 40°C for 1 wk, and determined the mass of each component. To estimate net N uptake by *S. missouriensis*, I determined the N content of goldenrod tissue using a Carlo-Erba combustive C-N-S autoanalyzer (Tilman and Wedin 1991a).

I estimated the mean relative growth rate of *S. missouriensis* (RGR, percent per week) for the period June–September 1990 from the initial (June 1990) and final (September 1990) biomass estimates using the following formula:

$$\text{RGR} = \frac{\ln(\text{mass}_{\text{final}}) - \ln(\text{mass}_{\text{initial}})}{\text{number of weeks}} \times 100.$$

Resource availability and nitrogen mineralization

I measured light availability, defined as the percentage of ambient light reaching the soil surface, in 1990 following larval feeding (June) and adult feeding (August). I made all measurements between 1000 and 1400 on cloudless days. I selected six locations in each plot by randomly choosing angles from true north and distances from a post that I placed in the center of the plot. I measured PAR above the plot and at each location at the soil surface with a point PAR sensor (LI-COR). I took the average value as the plot's response.

I used a procedure similar to that described in Tilman and Wedin (1991a) to estimate available soil N (as nitrate and ammonium) and in situ N mineralization. In April, June, July, August, and September of 1990 I collected six 1.75 cm diameter \times 20 cm deep soil cores from random locations (chosen as described above) within each plot. I filled holes with soil from pocket gopher mounds and marked them to avoid resampling. I homogenized the soil from each core, and immediately placed a subsample of it into a vial containing 50 mL of 0.02 mol/L KCl. I dried the remainder of the soil at 105°C for 24 h to estimate soil water content. The vials containing soil and KCl were shaken for 30 min upon return to the laboratory and allowed to settle overnight at 4°C. If the supernatant could not be analyzed the following morning then I froze it. The supernatant's nitrate and ammonium content was determined using an AlpKem autoanalysis system. I used the mean of the six cores as the plot's response.

To estimate in situ N mineralization, I randomly selected one of the six locations sampled for available N in each plot, and inserted a 2 cm diameter \times 20 cm deep PVC (polyvinyl chloride) plastic tube adjacent that location. The tubes were loosely capped and had slits in their sides for ventilation. These tubes excluded plant roots so that N production could be estimated without plant uptake. I determined the N content of the soil in the tube as described above. I determined N mineralization during four intervals: September 1989–April 1990, April–June 1990, June–August 1990, and August–September 1990. I estimated net annual

in situ N mineralization for each plot as the sum of the N mineralization during these intervals.

Invasion of experimental plots

I collected the aboveground parts of all invading plants during the 1990 growing season in early June, July, and mid-August. I sorted them to the most narrow taxonomic level possible (usually species). I then dried them for 1 wk at 40°C and weighed them to the nearest 0.01 g. If a species weighed <0.01 g, then I simply recorded it as present.

Nitrogen uptake

I estimated net N uptake by *S. missouriensis* in each plot for the periods September 1989–June 1990 (end of larval feeding period) and June 1990–September 1990. Net N uptake for the latter period was simply the difference in the mass of N in goldenrod tissue (including litter for September 1990) between the two sampling dates. For the earlier period I estimated the mass of N in goldenrod tissue in September 1989 as:

$$\begin{aligned} \text{total plant N} = & \text{belowground N} \\ & + \text{N remobilized from leaves} \\ & \text{before abscission.} \end{aligned}$$

The N content of *S. missouriensis* stems in 1989 was negligible (Brown 1992) and I assumed that N in inflorescences was not remobilized. Since goldenrod litter in September 1989 consisted almost entirely of recently abscised leaves, I estimated N remobilization from the leaves that remained on the plant as:

$$\text{N remobilization} = \frac{(\%N \text{ in leaves} - \%N \text{ in litter})}{\%N \text{ in leaves}}.$$

I computed the mean remobilization for each folivory treatment and used that value for all plots assigned to that folivory treatment.

Statistical analysis

I analyzed the data from this experiment using multiple regression. The *t* statistic reported in the *Results* is that for coefficient of the dummy variable *Tri*(+) – *Tri*(–) in the regression model after inclusion of block effects, gopher damage, and other background variables. Data for invader biomass, annual nitrification, and annual mineralization were ln-transformed for analysis; the statistics for these data shown in the results were back transformed.

RESULTS

Leaf damage by *T. canadensis* and *S. missouriensis* production

Goldenrod in *Tri*(+) plots suffered higher leaf consumption by both *Trirhabda* larvae and adults than did that in *Tri*(–) plots in 1990 (Table 1), but the difference following larval feeding was far more striking. Folivory by *Trirhabda* larvae reduced leaf, root,

TABLE 1. Leaf consumption by *Trirhabda canadensis* and its effects on mean leaf, root, and total biomass of *Solidago missouriensis* at two times in 1990 (means \pm 1 SE).

Response	+ <i>Trirhabda</i>	– <i>Trirhabda</i>	<i>t</i> (df = 28)
June, after feeding by larvae			
Leaf area consumed (%)	92.96 \pm 3.17	7.32 \pm 2.80	18.70****
Leaf biomass (g/m ²)	16.36 \pm 4.73	168.72 \pm 28.69	–7.43****
Root biomass (g/m ²)	30.82 \pm 4.29	91.36 \pm 16.62	–4.16***
Total biomass (g/m ²)	101.40 \pm 16.72	406.37 \pm 60.74	–5.99****
August/September, after feeding by adults			
Leaf area consumed (%)	16.49 \pm 1.27	9.45 \pm 0.45	3.97***
Leaf biomass (g/m ²)	130.62 \pm 14.58	173.62 \pm 21.21	–1.21
Root biomass (g/m ²)	72.04 \pm 11.11	140.80 \pm 21.00	–3.38**
Total biomass (g/m ²)	305.81 \pm 37.73	747.31 \pm 87.87	–5.43****

** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

and total biomass of goldenrod. Differences in root and total biomass persisted into September 1990, but the difference in leaf biomass did not.

Availability of resources

Folivory by *Trirhabda* increased both light penetration and soil water content in goldenrod monocultures in 1990 (Table 2). Folivory did not affect extractable soil N concentration, but the concentration of nitrate was higher in *Tri*(+) plots than in *Tri*(–) plots. Differences in soil water and nitrate content between *Tri*(+) plots and *Tri*(–) plots were accentuated in June and July of 1990 following heavy defoliation by *Trirhabda* larvae.

Invasion of experimental plots

A total of 42 plant species invaded the experimental goldenrod plots in 1990. Folivory by *Trirhabda* increased mean probability of invasion for the 21 species that invaded at least 25% of the plots (Table 3). The species richness and biomass of the invading plant assemblage were both higher in *Tri*(+) plots than in *Tri*(–) plots. The relative growth rate of goldenrod in *Tri*(+) plots was higher than that of goldenrod in the *Tri*(–) plots. Erect forbs constituted a higher proportion of

aboveground invader biomass in *Tri*(–) plots than in *Tri*(+) plots, while prostrate or creeping forbs showed the opposite response (Table 3). The most common erect forbs invading experimental plots were *Ambrosia artemisiifolia*, *Erigeron* spp., and *Artemisia caudata*, while the predominant prostrate species were *Euphorbia* spp. and *Mollugo verticillata*.

Nitrogen mineralization and uptake

Annual rates of N mineralization and nitrification were higher in *Tri*(+) plots than in *Tri*(–) plots (Table 4). Folivory by *Trirhabda* larvae reduced net N uptake by *S. missouriensis* during the interval September 1989–June 1990. Goldenrod in *Tri*(–) plots gained N while that in *Tri*(+) plots lost N during that interval. In contrast, N uptake between June and September 1990 did not differ between the folivory treatments.

DISCUSSION

Folivory and resource availability

Folivory by *Trirhabda canadensis* simultaneously increased the environmental availability of three resources that influence plant growth and community structure: light, water, and nitrogen. Studies docu-

TABLE 2. Impact of grazing by *Trirhabda canadensis* upon availability of light, water, KCl-extractable soil nitrogen (NH₄-N + NO₃-N), and soil NO₃-N in experimental goldenrod monocultures in 1990 (mean \pm 1 SE).

Response	+ <i>Trirhabda</i>	– <i>Trirhabda</i>	<i>t</i> (df = 28)
Light penetration to soil surface (%)			
June 1990, after larval feeding	90.09 \pm 1.89	32.63 \pm 5.12	11.66****
August 1990, after adult feeding	62.92 \pm 4.55	36.96 \pm 3.30	3.82***
Soil water content (% by mass)			
1990 average	6.80 \pm 0.10	6.12 \pm 0.25	3.29**
June and July only	5.09 \pm 0.12	3.69 \pm 0.24	6.40****
KCl-extractable soil N (mg/kg soil)			
1990 average	1.57 \pm 0.19	1.43 \pm 0.34	0.67
June and July only	2.66 \pm 0.35	2.06 \pm 0.54	1.42
Soil NO ₃ -N (mg/kg soil)			
1990 average	0.267 \pm 0.038	0.116 \pm 0.038	2.54*
June and July only	0.490 \pm 0.074	0.121 \pm 0.045	3.27**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

TABLE 3. Responses of vegetation to grazing by *Trirhabda canadensis* in experimental goldenrod monocultures in 1990 (means \pm 1 SE).

Response	+ <i>Trirhabda</i>	– <i>Trirhabda</i>	<i>t</i> (df = 28)
Invasion probability† (% plots invaded)	28.87 \pm 1.83	19.64 \pm 2.08	4.27***
Species richness (no./plot)	14.1 \pm 0.8	8.8 \pm 0.8	5.67****
RGR of <i>S. missouriensis</i> (%/wk)	12.67 \pm 1.40	6.63 \pm 1.88	2.62*
Biomass of invaders (g/plot)	11.59 \pm 1.40	1.59 \pm 0.42	7.34****
Composition of invaders (%)			
Erect forbs	31.02 \pm 4.13	53.29 \pm 6.69	–2.96**
Graminoids	42.51 \pm 4.54	37.36 \pm 6.09	0.97
Prostrate and creeping forbs	26.47 \pm 3.79	9.35 \pm 2.55	2.71*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.† Paired *t* test with df = 20.

menting the impact of grazers upon available resource levels in terrestrial plant communities are rare. Vertebrate grazers can alter the availability of water (Archer and Detling 1986, Svejcar and Christiansen 1987) and N (Inouye et al. 1987a), while grazing by grasshoppers increased N availability in some CCNHA old fields (M. Ritchie, *personal communication*). Elevated stream nutrient concentrations (Swank et al. 1981, Swank 1988) and increased deposition of frass, leaf parts, and body parts (Ohmart et al. 1983, Lamb 1985, Hollinger 1986, Schowalter et al. 1986) during insect outbreaks indirectly suggest that insect grazing might affect available soil nutrient levels in other habitats.

Indirect evidence suggests that elevated available resource levels may generally accompany herbivore activity. Root biomass, which is positively correlated with nutrient uptake capacity (Tilman and Wedin 1991a), generally declines following grazing or clipping (Biswell and Weaver 1933, Jameson 1963, Belsky 1986, Ruess 1988). Increases in the N content of vegetation (Cargill and Jefferies 1984a, Ruess 1988, Day and Detling 1990, Holland and Detling 1990), the rate of nutrient uptake by roots (Chapin and Slack 1979, Jaramillo and Detling 1988, Polley and Detling 1988, 1989, Ruess 1988), the rate of nutrient cycling (McNaughton 1985, Ruess 1987, Holland and Detling 1990), and primary productivity (Cooper 1973, McNaughton 1979, Lehman 1980, Sterner 1986, Carpenter and Kitchell 1988, Hik and Jefferies 1990, Dyer et al. 1991b) are all associated with herbivory. Available resource levels are important determinants of the establishment and performance of plants and of the out-

come of their interspecific interactions (Harper 1977, Tilman 1982, 1988, Inouye and Tilman 1988, Carson and Pickett 1990, Tilman and Wedin 1991b). When possible, investigators should directly measure resource availability as a potential underlying mechanism by which herbivores influence plant community structure. Since resource availability depends upon the interaction of many processes influencing both the supply and removal of nutrients (Tilman 1982), one cannot accurately infer herbivory's aggregate impact upon resource availability by determining its influence upon a subset of these processes.

Both reduced consumption and increased production of resources probably increased resource availability following defoliation (Fig. 2). Tilman (1988) argued that high loss rates, by reducing the biomass of resource-harvesting organs, should impede resource consumption and thereby yield higher resource availability. This prediction was supported by this study. It is not surprising that the nearly complete removal of goldenrod leaves by *Trirhabda* larvae caused a large increase in light penetration in *Tri*(+) monocultures. Leaf loss may also have reduced transpiration and thereby increased water availability in *Tri*(+) plots (Archer and Detling 1986, Svejcar and Christiansen 1987). The negative net N uptake by goldenrod in *Tri*(+) plots coincided with a large reduction in root biomass in those plots. Varying the assumptions I used to estimate the size of the goldenrod N pool in September 1989 (see *Methods*) did not affect this qualitative result. Root loss like that observed in the *Tri*(+) plots generally accompanies that of leaves (Biswell and Weaver

TABLE 4. Impact of grazing by *Trirhabda canadensis* on annual rates of nitrogen mineralization and nitrification and upon nitrogen uptake by *Solidago missouriensis* in experimental goldenrod monocultures (means \pm 1 SE).

Response	+ <i>Trirhabda</i>	– <i>Trirhabda</i>	<i>t</i> (df = 28)
N mineralization rate (mg·kg ⁻¹ ·y ⁻¹)	9.01 \pm 1.11	5.88 \pm 1.08	2.05*
Nitrification rate (mg·kg ⁻¹ ·y ⁻¹)	4.80 \pm 0.40	3.46 \pm 0.32	2.64*
N uptake by <i>S. missouriensis</i> (g/m ²)			
September 1989–June 1990	–0.98 \pm 0.26	2.87 \pm 0.94	–5.22****
June 1990–September 1990	4.51 \pm 0.71	3.65 \pm 1.08	1.13

* $P < 0.05$, **** $P < 0.0001$.

1933, Troughton 1957, Jameson 1963, Belsky 1986) because reduced photoassimilate production by leaves cannot support the current root system (Milthorpe and Davidson 1966, Chapin and Slack 1979) and stored or newly acquired carbon and nutrients are used to reconstruct lost photosynthetic tissues (Gifford and Marshall 1973, Ryle and Powell 1975, Richards 1984, Welker et al. 1987, Dyer et al. 1991a, Brown 1992).

Several factors may have augmented the rate of N mineralization in defoliated plots. First, the large increase in light availability following larval feeding probably raised soil temperature in *Tri*(+) plots (Vitousek and Mattson 1985). Increased temperature, coupled with elevated soil water content, probably created a highly favorable environment for microbial activity (Bormann and Likens 1979, Vitousek et al. 1979, Vitousek and Mattson 1985). The large flux of readily mineralizable frass, leaf parts, dead roots, and insect body parts associated with *Trirhabda* folivory would have provided ample substrate to fuel the increased mineralization rate in defoliated plots.

Increased rate of nutrient uptake may be important in spurring regrowth after defoliation (Chapin and Slack 1979, Jaramillo and Detling 1988, Polley and Detling 1988, 1989). Goldenrod in the two folivory treatments had similar net N uptake following larval feeding despite the reduced root biomass in *Tri*(+) plots. Similar N uptake suggests that roots in the *Tri*(+) plots acquired N more rapidly than did those in *Tri*(-) plots. More rapid N uptake and increased allocation of N to leaves (Brown 1992) may have augmented the RGR of goldenrod in *Tri*(+) plots (Tilman 1988). Goldenrod roots in *Tri*(+) plots may have also acquired N more rapidly than those in *Tri*(-) plots during the larval feeding period. However, the N uptake rate in *Tri*(+) plots was not sufficiently high to prevent loss of nutrient capital while *Trirhabda* larvae consumed *S. missouriensis* (cf. Jaramillo and Detling 1988, Ruess 1988). Increased shoot sink strength or root permease content may contribute to increasing rates of nutrient uptake following defoliation (Gifford and Evans 1981, Clarkson 1985). This study suggests that increased ambient nutrient availability may also contribute to this phenomenon. Increased water availability following defoliation may enhance plant regrowth (McNaughton 1979, 1983, Svejcar and Christiansen 1987), but the link between soil water content and growth rate is far from clear (Jantti and Kramer 1956, White and Brown 1972, Wolf and Parrish 1982, Archer and Detling 1986). Since the availability of light, water, and nitrate changed simultaneously, this study cannot reveal whether elevated soil water availability augmented the RGR of *S. missouriensis* following larval defoliation.

Several factors hampered detection of differences in N availability by this study. First, both the plants that invaded the experimental plots and those growing immediately outside them could consume N within the plots. Often >10 g of aboveground invader biomass

grew within *Tri*(+) plots. *Poa pratensis* and *Agropyron repens* were often invaded by rhizomes that grew beneath the flashing surrounding a plot, so it is likely that their roots could do the same. Differences in N availability between the two folivory treatments might have been more pronounced if I had excluded all invaders. A second obfuscating influence was gopher activity. Although gophers did not preferentially attack either folivory treatment and had little effect upon any response variable, gophers deposited N-poor CCNHA subsoil on the surface (Inouye et al. 1987a). At a minimum, gopher activity might have increased interplot variation, making differences in N availability more difficult to detect. At worst, deposition of N-poor soil in defoliated plots may have diluted any increase in available soil nitrogen content associated with *Trirhabda* folivory. A third problem was that the bulk of the available soil N was present as ammonium. The concentration of this ion is generally more variable than that of nitrate in the soils of CCNHA (A. El Haddi, personal communication). The concentration of ammonium was also more variable than that of nitrate in my experimental plots (Brown 1992). In addition, the factors that augmented N mineralization in *Tri*(+) plots also stimulated the activity of nitrifying bacteria (Vitousek et al. 1979). These organisms reduced the availability of ammonium while generating the observed differences in nitrate availability. Finally, a larger portion of the mobile nitrate pool may have leached from *Tri*(+) plots than from *Tri*(-) plots because of the low root biomass in *Tri*(+) plots (Vitousek et al. 1979, Tilman and Wedin 1991a, Brown 1992).

Invasion of experimental plots

The observed differences between the folivory treatments in species invasion and the RGR of *S. missouriensis* are consistent with predictions (Fig. 1). The most frequent invaders of my goldenrod monocultures are also common colonists of newly abandoned fields and gopher disturbances at CCNHA (Tilman 1983, 1988). These habitats are characterized by relatively high availability of both light and N. Since most of the invaders probably germinated from the seed bank, other factors associated with the folivory treatments, such as increased soil temperature, may also have played a role in generating the observed differences (Grubb 1977). The dominant prostrate species, *Euphorbia* spp. and *Mollugo verticillata*, both grow in mats from a small central taproot. The relatively high allocation to photosynthetic tissues and low allocation to stems and roots in these species may confer both high maximal RGR (Tilman 1988, Poorter and Remkes 1990) and high colonization ability (Gleeson and Tilman 1990). Species with such characteristics often are transient dominants in plant communities with perturbations that increase resource availability (Tilman 1988). My results were also similar to those reported by Carson

and Pickett (1990), who observed an increase in the relative abundance of *Fragaria*, a creeping plant, in the understory of *Solidago altissima* stands in response to experimental resource augmentation. Across many diverse habitats, patches with high resource availability generated by disturbance or consumer activity often have higher relative abundance of rapidly growing species than do undisturbed patches or those less influenced by consumers (Grime and Hunt 1975, Grime 1977, Lubchenco 1978, Sousa 1979, McNaughton 1984, Schoenberg and Carlson 1984, Hart 1985, Carpenter 1986, 1990, Sterner 1986, Power et al. 1988, Noy-Meir et al. 1989, Olson and Lubchenco 1990).

Studies from a variety of habitats suggest that the impact of herbivory upon plant communities is a consequence of its influence upon the availability of resources such as light (Ellison 1960, McNaughton 1984, 1992, Carpenter 1986, 1990), space (Lubchenco 1978, Power et al. 1988, Olson and Lubchenco 1990), and nutrients (Cargill and Jefferies 1984a, b, Sterner 1986, 1990). Changes in plant community structure caused by herbivores have been mimicked by experimental resource augmentation in forests (Mattson and Addy 1975, Waring and Pitman 1985, Romme et al. 1986, Veblen et al. 1991), heathlands (Heil and Diemont 1983, Berdowski and Zelinga 1987), and *Solidago* stands (McBrien et al. 1983, Armesto and Pickett 1985, Carson and Pickett 1990). These studies and my results suggest that examination of how herbivores affect resource availability can help elucidate physiological and ecological responses of plants and plant communities to herbivory. Moreover, a focus on resource availability may help to unify different research avenues within plant ecology. For example, both herbivory and abiotic or biotic disturbance can alter the mean or variance of resource availability in addition to resource availability ratios (Sousa 1984, Canham and Marks 1985, Carson and Pickett 1990), and both can affect plant community structure in similar ways (Cooper 1973, Connell 1978, McNaughton 1979, Hilbert et al. 1981, Tilman 1982, 1988, Carpenter and Kitchell 1984, Armesto and Pickett 1985, Carson and Pickett 1990, Huntly 1991). Acquisition of, and competition for, resources is an important determinant of plant performance (Grime 1977, Harper 1977, Tilman 1982, 1988). Knowledge of the effects of herbivory or abiotic disturbance on resource availability may lead to predictions about how these processes and their perturbations will affect individual plants, species, and the outcome of interspecific interactions. Such information may have great practical value in such areas as prairie restoration or rangeland management (Levin 1993). In addition, examining resource availability provides plant ecology with a mechanistic link between the physiological and ecosystem scales of inquiry (Tilman 1985, Holland et al. 1992). Huntly (1991) suggested that plant communities exhibit similar responses to herbivores in a variety of ecosystems. Perhaps a consistent effect of

herbivory upon resource availability is one reason for her observation.

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