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Interactions between goldenrod (*Solidago altissima* L.) and its insect herbivore (*Trirhabda virgata*) over the course of succession

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Abstract Consumers can mediate the composition of plant communities and alter ecosystem processes. Although herbivores usually increase N availability in the short term, they might decrease it in the long term. I investigated the long-term effect of insect herbivores on leaf tissue quality and soil N availability in goldenrod (*Solidago altissima*) fields using two approaches: (1) I compared plots from which herbivores had been excluded for 17 years with adjacent plots that had experienced normal levels of herbivory, and (2) I examined a chronosequence of nine goldenrod fields representing three successional stages: early, middle, and late. These parallel approaches showed that, in the long term, herbivores decrease the quality of leaf litter and soil N availability in goldenrod fields. These long-term effects appear to compensate for various short-term effects that increase N availability in the soil (e.g., added frass, increased light penetration). Furthermore, herbivores decrease leaf litter quality and N availability by reducing the quality of leaf tissue *within the same species*. This pattern may result from insect herbivores preferentially grazing on plants with a high N content thereby increasing the amount of recalcitrant litter over the course of succession.

Key words Herbivores · Nitrogen · Succession · *Solidago* · Positive feedback

Introduction

Mounting evidence that herbivores play a crucial role in mediating plant competition and nutrient dynamics makes focusing on consumers essential to fully understand the mechanisms that drive plant community composition over time (Mattson and Addy 1975; MacNaughton 1985; Chapin et al. 1986; Naiman et al. 1986; Vitousek et al. 1987; Pastor and Naiman 1992; Pastor et al. 1993; Ritchie and Tilman 1995; Ritchie et al. 1998). Herbivore preference for particular plant species can alter plant community composition and nitrogen cycling (Belsky 1986; Bryant et al. 1991; McInnes et al. 1992; Pastor et al. 1993; Ritchie et al. 1998). For instance, Ritchie et al. (1998) found that excluding herbivores from experimental plots for 7 years increased legume cover, the amount of N in litter, and N availability in the soil.

Selective herbivory of high-quality individuals or plant parts of a monodominant species also has the potential to reduce the quality (N content) of litter and lead to slower nitrogen cycling. Herbivores may prefer to graze on plants with high N content and, as an indirect result, decrease the quality of the leaf litter. Recalcitrant litter (high C:N ratios) increases microbial nitrogen demand and may reduce the amount of N available to plants. This positive feedback mechanism could further reduce plant leaf tissue quality over the course of succession.

This research examines how the interactions between nitrogen availability, leaf tissue quality, and insect herbivore pressure vary over time in old fields dominated by tall goldenrod (*Solidago altissima* L.). Tall goldenrod is a native, clonal rhizomatous perennial (Cronquist 1980; Werner et al. 1980) with a highly diverse insect fauna (>100 species) (Root and Cappuccino 1992; Root 1996). Goldenrods thrive in disturbed environments, commonly dominating old fields throughout the northeastern United States. Fields dominated by goldenrod provide an ideal system for studying the interaction between nutrient dynamics and herbivory over time for several reasons. First, the natural history of many of the goldenrod insects has been studied (Messina 1978; Messina and Root 1980; McBrien et al. 1983; McEvoy 1986, 1988; Capuccino 1987, 1991; Hamilton 1989; Root and Capuccino 1992; Abrahamson and Weis 1996). Second, there is evidence that some of these herbivores, in particular the chrysomelid beetle *Trirhabda virgata*, have an

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effect on plant community composition and nitrogen cycling in goldenrod fields (McBrien et al. 1983; Brown 1994; Carson and Root, in press). Finally, there is some indication that these effects can alter the course of succession (McBrien et al. 1983; Root 1996; Carson and Root, in press).

Insect herbivores, and in particular the specialist chrysomelid beetles *T. virgata* and *Microrhapala vittata*, are likely to outbreak during the 20 years or more during which goldenrod occupies a site (Root and Cappuccino 1992; Carson and Root, in press). These outbreaks can completely inhibit flowering and severely stunt vegetative growth (McBrien et al. 1983; Root 1996). The reduced vigor of goldenrod after outbreaks allows other species present in the understory to become dominant (McBrien et al. 1983; Brown 1994; Carson and Root, in press). In the absence of herbivory, tall, dense goldenrod stands prevent light penetration to the understory and the establishment of woody vegetation (Carson and Root, in press).

Goldenrod herbivores can also affect the composition of the plant community indirectly by changing nutrient levels. The availability of resources in turn influences the growth and interspecific interactions of terrestrial plants (Harper 1977; Tilman 1988). In goldenrod fields, *T. virgata* folivory increases nitrogen availability in the short term as a result of (1) increased light penetration and soil water content which in turn increase microbial activity, (2) reduced goldenrod N uptake (Brown 1994), and (3) increased N inputs into the soil as insect frass and body parts. The long-term effect of herbivores on N cycling in goldenrod fields, however, remains unknown.

Basic approaches

In this study, I examined the interactions of nitrogen cycling, leaf tissue quality, and herbivore abundance over time using two approaches.

(1) I directly measured these variables in a chronosequence of old fields representing different successional ages (space for time substitution, sensu Pickett et al. 1987). I randomly selected a total of nine field sites representing three different successional stages: three early (1–2 years since abandonment), three middle (5–10 years), and three late (invasion by woody species evident) dispersed throughout Tompkins County in central New York state. All these old fields were dominated by *Solidago* and *Aster* spp. To avoid topographic and anthropogenic effects, fields were selected using the following criteria: (1) the area of the field exceeded 7000 m^2, (2) the population of *S. altissima* exceeded 5000 ramets, (3) the site was isolated from road dust and pesticide drift, and (4) the site was relatively level and well drained.

(2) I took advantage of a long-term experiment on the effects of removing insects on plant community structure, composition, and diversity (Root 1996; Carson and Root, in press). This long-term experiment had been conducted at Whipple Field, northeast of Ithaca, New York, formerly a neglected hay meadow that was abandoned in 1970 and mowed once again sometime prior to 1975 (Messina and Root 1980). By comparing plots that had been protected from herbivory for the previous 17 years to adjacent plots that had experienced normal levels of herbivory throughout that period, I was able to observe directly the effects of herbivores on leaf tissue quality and soil processes at this site. The character and intensity of the herbivore pressure experienced by the plants in these plots are known from long-term censuses of the insects at this site (Root 1996; Carson and Root, in press). Herbivore damage was typical for goldenrod stands over a broad regional area (Root and Cappuccino 1992; Root 1996).

These two approaches allowed me to infer how the long-term effects of herbivory on leaf tissue quality and nitrogen cycling I observed at Whipple Field may translate into the patterns observed in the chronosequence of old fields. I first compared the quality of leaf tissue over the course of succession in the nine fields representing a successional sequence with that of goldenrods in sprayed (no historical herbivory) and unsprayed (historical herbivory) plots at Whipple Field. I followed the same approach to examine nitrogen cycling processes. In a second, and more mechanistic set of experiments, I manipulated the level of contemporaneous herbivory and nitrogen availability in the sequence of nine fields to dissect the interactions between herbivore pressure and nitrogen availability over the course of succession.

I also examined the effects of successional age on the fitness of *T. virgata* using data from both the chronosequence of fields and the plots at Whipple Field. I compared the fecundity of *T. virgata* adults in the chronosequence of old fields and the growth of *T. virgata* larvae that had been fed leaf tissue from the Whipple Field sprayed and unsprayed plots. By focusing on one herbivore for which there is extensive population data, the chrysomelid beetle *T. virgata* (Messina and Root 1980; Messina 1982; Hamilton 1989; Root and Cappuccino 1992; Herzig 1995; Herzig and Root 1996), I hoped to obtain better insights into the mechanisms that determine herbivore pressure and abundance over the course of succession.

Materials and methods

Effects of nitrogen availability on goldenrod biomass, N cycling, and herbivory

To determine the effects of N availability on goldenrod leaf tissue quality (i.e., C:N ratio), I fertilized 1-m^2 plots in each of the nine fields in the chronosequence with 6 g of slow-release ammonium nitrate (21 kg/ha ammonium nitrate-N). This fertilization was intended to elucidate how fields at various successional ages respond to increased nitrogen availability and to determine if the ability of goldenrod to take up nitrogen changes with successional time.

Because fertilization can simultaneously result in changes in herbivory rates and nitrogen cycling, I crossed the fertilizer treat-

ment with insect removal in a 2×2 fully factorial design. The no-insect plots were sprayed with fenvalarate, a pyrethroid insecticide, every 2 weeks to eliminate larvae emerging from eggs from previous years. This insecticide does not affect goldenrod growth, is not phytotoxic, does not alter microbial biomass, and is quickly biodegraded in the soil with no effect on total soil nitrogen availability (the caveats and rationale for using fenvalerate are discussed in Root 1996 and Carson and Root, in press). Each treatment was replicated eight times in each of the selected fields. At the end of the season, an area of 0.25 m^2 in each of the 1-m^2 plots was harvested by clipping all the aboveground plant material. Goldenrod flowers, stems, and leaves were separated, dried at 60°C for 48 h and weighed. The biomass of the four treatments was compared to determine the effects of succession, fertilizer, and pesticide. All interactions between factors were also tested. All data were analyzed using a mixed linear model nested analysis of variance (ANOVA). The Mixed Procedure (SAS 1997) is designed to handle both fixed and random effects. In the event that the data are not completely balanced, this procedure better approximates the *F*-distribution than the SAS Proc GLM (Littel et al. 1996). Successional stage, fertilizer, and pesticide were considered fixed effects. Field(site) was considered a random factor nested within successional stage.

Changes in plant tissue quality across succession

To investigate how the nutritional quality of goldenrod changes during succession, I harvested goldenrod leaves from 20 randomly chosen shoots for the four treatments described above for each of the sites and measured total N and total C. Total N is important, as nitrogen is a limiting factor for most herbivorous insects (Mattson 1980). Furthermore, the C:N ratio of leaf tissue is important in determining the rate of nutrient cycling in the soil (Aber and Melillo 1980). Samples were collected once in late June and again in late August to reflect the host plant nutritional quality that the goldenrod insects are likely to encounter in their larval and adult stages.

I also examined the direct long-term effects of insect suppression on leaf tissue quality by collecting *S. altissima* leaves from both the 19 sprayed and 19 unsprayed plots at Whipple Field. I used samples from a composite collection of leaves from all the plots for the analysis. All leaf samples were dried for 48 h at 60°C, ground, and analyzed for nutrient content using a Carlo Erba CN analyzer. All C:N ratio data were log-transformed for the statistical analyses.

Changes in nitrogen cycling

For each of the fields included in the study, I collected five soil cores, 3.8 cm in diameter and 10 cm in depth. Samples were air dried and analyzed for pH using an Accumet pH/conductivity meter. Total nitrogen and carbon were measured using a Carlo Erba CN analyzer. An index of nitrogen availability at each site was determined using ion exchange resin bags. The amount of N captured in resin bags depends primarily on the N mineralization rate, water movement through the bags, and competition for nutrients with microbes and plants (Binkley 1984), the same processes that affect the supply of ions to root surfaces. Although the relative importance of these factors might be different for resins and roots, resin bags measure differences among treatments accurately (Binkley et al. 1992).

The bags were placed 10–15 cm below the organic horizon in early June (Binkley et al. 1992) and were removed in late August. A second set of resin bags was placed in plots fertilized with ammonium nitrate as described above. All resins were washed with deionized water and extracted with 0.1 M KCl/2 M NaCl (Giblin et al. 1994). The extractant was filtered and analyzed using an Alpkem Flow Solution autoanalyzer (Perstop Analytical USA).

I also measured the effects of long-term insect suppression on N availability by placing five resin bags in both sprayed and unsprayed plots at Whipple Field. Five soil cores from five randomly chosen sprayed and unsprayed plots were also taken to determine the impact of long-term herbivory on pH, C, and N content of the soil.

Insect abundance and performance

I sampled insects twice in the summer, late May and mid July, to quantify the abundance of both larvae and adults and to obtain a direct measure of herbivore abundance in the chronosequence of old fields. Transects were established at each of the fields. I walked the transect, stopped every fifth stride, chose a goldenrod stem randomly by pointing a stick to the ground while looking in the direction of the transect. The goldenrod closest to the stick was inspected carefully and insects found on it were recorded. A total of 50 plants were sampled in each field for each sampling period. I calculated herbivore load by dividing the total number of insects found on a shoot by its height. This method allowed me to standardize the abundance of insects across fields. Root and Cappuccino (1992) used this method for similar purposes and found that the results were comparable to those obtained using total insect abundance per ten plants. Furthermore, the fact that leaf biomass per centimeter of stem did not differ between successional stages (M. Uriarte, unpublished data) makes me confident that the data on insect abundance reflect true differences between fields and not changes in the amount of foliage per centimeter of stem across successional stages.

To investigate the variability in adult fecundity between fields of various successional ages, I collected at least ten adult gravid *T. virgata* females from each field prior to dispersal, dissected them, and counted the number of eggs. I also investigated whether the nutritional quality of *S. altissima* in sprayed and unsprayed plots affects feeding efficiency and growth of *T. virgata* using methods developed by Brown and Weis (1995). In early spring 1997, I collected second-instar *T. virgata* larvae. A set of these larvae was dried and weighed. The remaining larvae were assigned to experimental treatments. Variability in initial weights can reflect true differences or the time since the larvae last fed. For this reason, I averaged the weight of 20 larvae collected at random and used the average as initial weight for both treatments. For each feeding trial, two second-instar larvae were starved for 24 h, then placed on a dish in the laboratory, where they were fed leaves from either the unsprayed or sprayed plots. A total of 20 larvae were assigned to feed on foliage from each treatment. Leaves were collected every morning between 9:00 and 10:00 a.m. and placed immediately in a dish with water. They were brought back to the laboratory and run through a leaf scanner to calculate total leaf area. A subset of the leaves was placed in Aquapiks and fed to the larvae. The remaining leaves were dried at 105°C for 24 h to estimate the water content and specific leaf mass of the leaves used in the performance trial. Trials continued for 10 days. At the end of the experiment, larvae were collected from each dish, dried at 40°C for 48 h, and weighed. Total leaf area removed was calculated by tracing the remaining leaf area in the scanner and comparing it to that measured prior to the trial. Total leaf mass consumed was calculated using the leaf material collected for each trial. The following performance indices were calculated: weight gain, relative growth rate, biomass conversion efficiency, and relative consumption rate (Waldbauer 1968; Slansky and Feeny 1977). I conducted ANOVA tests to analyze the data on larval growth and performance indices.

Results

Chronosequence of old fields

Plant biomass

Individual flower and stem weight were highest in early succession and decreased in mid and late successional sites (Tables 1, 2).

Fertilization increased flowering and flower and stem weight in the presence of herbivores, but not in pesticided plots, indicating that herbivory may increase nitrogen demands (Tables 1, 3).

Table 1 Results of three-way ANOVA analyzing the effects of succession stage, pesticide, and fertilizer on C: N ratio, percent flowering stems, and average goldenrod flower, stem, and leaf biomass in a 0.25-m^2 area. For individual variables, *P*-values at α=0.05 are statistically significant; for interactions, α=0.10 was used

Response variable	*F*	*df*	*P*
Percent flowering stems			
Succession	1.73	2,6	0.258
Pesticide	3.31	1,6	0.118
Fertilizer	0.35	1,6	0.57
Pesticide×fertilizer	8.59	1,6	0.0262
Pesticide×succession	0.22	1,6	0.8057
Fertilizer×succession	1.04	1,6	0.4083
Pesticide×fertilizer×succession	0.34	1,6	0.72
Flower biomass			
Succession	6.81	2,6	0.028
Pesticide	2.73	1,6	0.25
Fertilizer	1.58	1,6	0.14
Pesticide×fertilizer	4.0	2,6	0.0923
Pesticide×succession	1.42	1,6	0.31
Fertilizer×succession	0.77	1,6	0.5
Pesticide×fertilizer×succession	0.15	2,6	0.86
Stem biomass			
Succession	8.25	2,6	0.019
Pesticide	1.31	1,6	0.29
Fertilizer	0.001	1,6	0.97
Pesticide×fertilizer	3,89	1,6	0.09
Pesticide×succession	0.62	1,6	0.56
Fertilizer×succession	1.14	1,6	0.37
Pesticide×fertilizer×succession	0.15	2,6	0.86
Leaf biomass			
Succession	4.34	2,6	0.068
Pesticide	0.06	1,6	0.81
Fertilizer	0.04	1,6	0.84
Pesticide×fertilizer	3.26	1,6	0.121
Pesticide×succession	1.0	1,6	0.42
Fertilizer×succession	0.92	1,6	0.449
Pesticide×fertilizer×succession	0.75	1,6	0.513
Log C:N ratio			
Succession	0.67	2,6	0.54
Pesticide	0.26	1,6	0.62
Fertilizer	0.02	1,6	0.89
Pesticide×fertilizer	3.71	1,6	0.1
Pesticide×succession	0.51	1,6	0.62
Fertilizer×succession	0.69	1,6	0.53
Pesticide×fertilizer×succession	0.54	1,6	0.61

Leaf tissue quality

Leaf tissue quality did not differ among the three stages of succession either in June or in September. Surprisingly, neither fertilization nor pesticide application had an effect on the C:N ratio of goldenrod leaf tissue across the chronosequence.

T. virgata *abundance and fecundity*

There was no difference in the abundance of *T. virgata* larvae between successional sites (Fig. 1a). The fecundity of *T. virgata* females was lower in late than in early and mid successional fields (Fig. 1b). Although this trend was not significant, the data may have been biased by my inability to find any gravid *T. virgata* females in two out of three late succesional fields. This result makes me suspect that late successional fields might be inhospitable to these insects. There was also a strong negative correlation between the number of eggs produced by mature *T. virgata* and the C:N ratio of leaf tissue (Pearson *r*=–0.68, Bartlet chi-square=4.165, *P*=0.041; Fig. 2).

Nitrogen cycling

Total soil N did not differ between the three succession stages. The amount of ammonium captured in resins was higher in fertilized plots (Fig. 3a). There were no differences in the amount of ammonium captured in control plots among the three succession stages. Nitrate in resins did not differ between succession stages but was higher in fertilized than in control plots (*F*=22.04, *df*=1,6, *P*=0.003; Fig. 3b). Resin bags in fertilized plots captured more ammonium and nitrate in mid and late successional sites although this trend was only marginally significant (Fig. 3a,b). The soil was most acid in mid and late successional sites (*F*=6.97, *df*=2,6, *P*<0.0273; Table 2).

Long-term suppression of insects at Whipple Field

Leaf tissue quality

Leaves from *S. altissima* growing in sprayed plots had a higher N content than those from plants growing in unsprayed plots (*F*=90.79, *df*=1,8, *P*=0.00001; Table 4).

Table 2 Means (with SE in parentheses) for soil pH, *Solidago altissima* leaf tissue C:N ratio, average flower, stem and leaf weight (g) and percent flowering stems in a 0.25-m^2 area. Different letters indicate that the means are significantly different at the α=0.05 significance level

Successional stage	Percent flowering stems	Flower weight	Stem weight	Leaf weight	C:N	pH
Early	0.79 (0.07)^a	1.84 (0.18)^a	7.9 (0.65) ^{a}	3.66 (0.35)^a	27.94 (1.54)^a	6.08 (0.19)^a
Mid	0.60 (0.07)^a	1.19 (0.18)^b	4.56 (0.65)^b	2.48 (0.35)^b	30.3 (1.54)^a	5.16 (0.19)^b
Late	0.69 (0.07)^a	0.87 (0.19)^b	4.78 (0.67)^b	2.29 (0.36)^b	29.8 (1.54)^a	5.29 (0.19)^b

Table 3 Means (with SE in parentheses) for *S. altissima* leaf tissue C:N ratio, average flower, stem, and leaf weight and percent flowering stems in a 0.25-m^2 area. Different letters indicate that the means are significantly different at the α=0.05 significance level for single-factor effects and α=0.10 for interactions after applying Fischer's LSD test for post hoc differences between means

Treatment	Percent flowering stem	Flower weight	Stem weight	Leaf weight	C:N
Control	0.59 (0.05)[a]	0.94 (0.13)[a]	5.19 (0.41)[a]	2.69 (0.24)[a]	28.32 (1.2)[a]
Pesticide	0.77 (0.05)[b]	1.49 (0.12)[b]	6.4 (0.41)[b]	2.96 (0.24)[a]	30.54 (1.2)[b]
Fertilizer	0.71 (0.05)[b]	1.37 (0.13)[b]	5.89 (0.41)[a]	3.05 (0.24)[a]	29.96 (1.2)[a]
Fertilizer and pesticide	0.7 (0.05)[a,b]	1.4 (0.12)[b]	5.59 (0.39)[b]	2.55 (0.23)[a]	28.57 (1.2)[a]

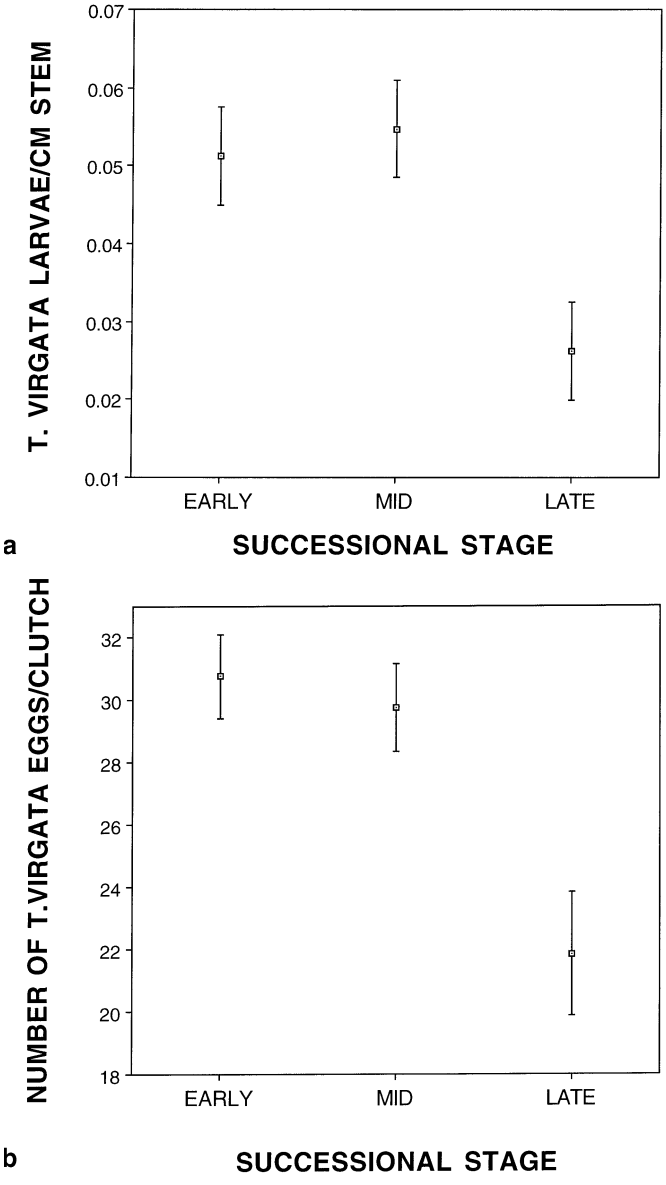

Fig. 1 **a** Means±SE for the number of *Trirhabda virgata* larvae per centimeter of *Solidago altissima* stem in early, mid, and late successional fields. **b** Means±SE for the number of eggs produced by *T. virgata* gravid females in early, mid, and late successional fields

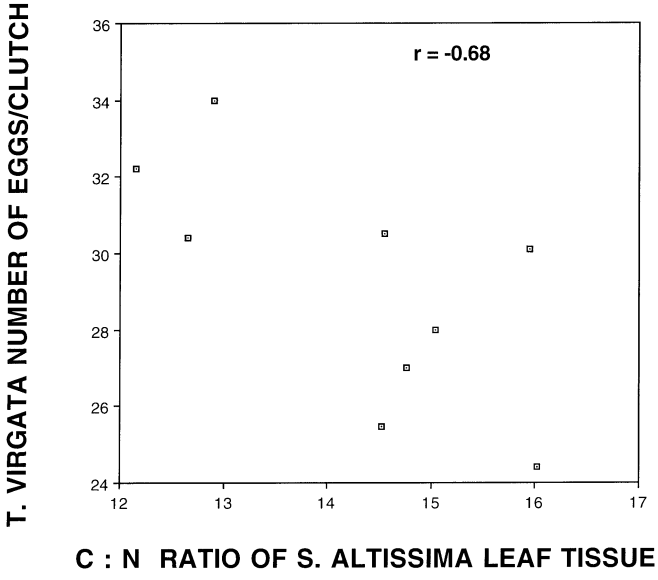

Fig. 2 Number of eggs of gravid *T. virgata* females versus the C:N ratio of *S. altissima* leaf tissue

The C:N ratio of *S. altissima* was higher in unsprayed plots (F=81.76, df=1,8, P=0.00002; Table 4).

Insect performance

Despite the fact that there was no difference in the total amount of foliage consumed by larvae subjected to a diet of leaves from sprayed and unsprayed plots, *T. virgata* larvae fed leaves from sprayed plants gained more weight than those fed from unsprayed plots (F=2.78, df=1,36, P=0.1; Table 5). Furthermore, 2 out the 20 larvae fed unsprayed leaves died during the trial, while all of the larvae fed on sprayed plants survived (chi-square=2.105, P=0.1468).

Relative growth rate, the mean compound growth rate required to produce the final mass of insect material, was higher for the larvae fed on the sprayed leaves (F=2.74, df=1,36, P=0.1; Table 5). Biomass conversion efficiency measures the efficiency with which an insect converts ingested biomass into insect biomass. Larvae fed on plants from the sprayed plots were more efficient than those raised on plants from the unsprayed plots (F=5.48, df=1,36, P=0.024; Table 5). Relative consumption rate,

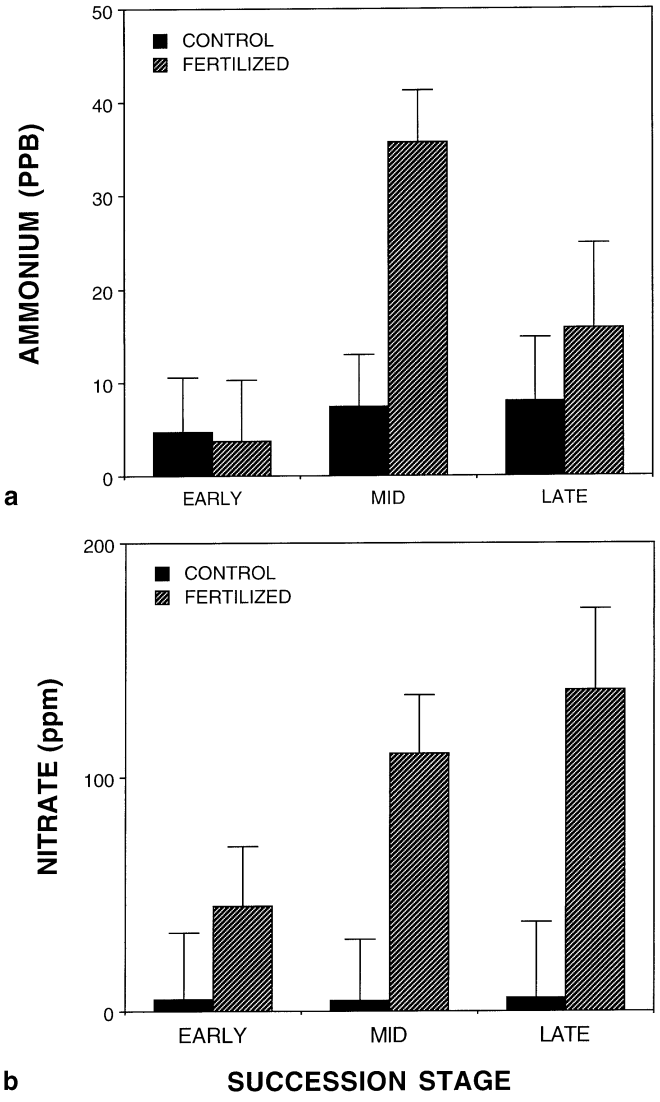

Fig. 3 Ammonium (in parts per billion) (**a**) and nitrate (in parts per million) (**b**) in control and fertilized plots in early, mid, and late successional *S. altissima* field

the mean daily leaf consumption per unit body mass over the course of the entire feeding trial, did not differ for the two treatments.

Nitrogen cycling

Soil pH did not differ between sprayed and unsprayed plots while total soil N was higher in sprayed plots (F=13.46, df=1,8, P=0.0063; Table 4). Resin bags in sprayed plots captured more ammonium than those in unsprayed plots (F=8.97, df=1,8, P=0.017; Table 4). There was no difference in the amount of nitrate in resin bags in sprayed and unsprayed plots.

Table 4 Means (with SE in parentheses) for soil characteristics and *S. altissima* leaf tissue quality in sprayed and unsprayed plots at Whipple Field

	Sprayed	Unsprayed
Nitrate	2.01 (0.89)	2.02 (0.89)
Ammonium	8.78 (1.15)	3.95 (1.15)*
Soil N	0.29 (0.016)	0.20 (0.016)*
Percent N in leaf tissue	1.70 (0.02)	1.42 (0.02)*
C:N of leaf tissue	27.07 (0.38)	31.96 (0.038*)

*$P \leq 0.05$

Table 5 Means (with SE in parentheses) for performance indices of *T. virgata* larvae fed *S. altissima* leaves from sprayed and unsprayed plots from Whipple Field

Response variable	Sprayed (n=20)	Unsprayed (n=18)
Weight gain (mg)	2.45 (0.26)	1.8 (0.28)*
Biomass consumed (mg)	29.83 (3.28)	35.01 (3.46)
Relative growth rate (%/day)	3.7 (0.35)	2.84 (0.37)*
Relative consumption rate (mg/g per day)	0.46 (0.04)	0.57 (0.05)
Biomass conversion efficiency (%)	8.67 (0.9)	5.85 (0.95)*
Final mass (mg)	7.69 (0.26)	7.05 (0.28)

*$P \leq 0.1$

Discussion

Effects of nitrogen availability on goldenrod leaf tissue quality and herbivory

All measures of goldenrod biomass and flower production were highest in the early successional field. Prior to abandonment, agricultural fields are usually tilled, limed, and fertilized while in cultivation. As a result, in the early stages of succession they tend to have a higher pH and provide a more favorable growing environment for goldenrods. The early successional fields in this study had higher pH although not higher total soil N. In early successional fields, resin bags in fertilized plots did not capture more N than those in control plots. Perhaps the higher pH in these fields facilitates microbial immobilization or plant uptake. Previous research has shown that soil pH has a strong effect on plant nutrient uptake (Marshner 1995).

The effects of fertilizer on biomass became apparent only when considered in conjunction with herbivore damage. Fertilized plants were able to maintain a higher percentage of flowering stems, and average flower and stem weight than unfertilized plants when under herbivore pressure. In contrast, plants lacking fertilizer suffered a decrease in all these variables in response to herbivore damage. These results confirm previous research showing that goldenrods adjust their response to contemporaneous herbivory to maintain established individuals at the expense of sexual reproduction (Meyer and Root 1996; Root 1996). This study, however, suggests that

goldenrods reduce allocation to sexual reproduction as a response to contemporaneous herbivory only when limited by nutrients.

Herbivores thereby affect reproductive effort and the plasticity of resource utilization in *S. altissima*. Stoll et al. (1998) showed that repeated mowing depleted *S. altissima* rhizomes of their stored resources. Herbivores may act in a similar manner by causing allocation of resources from rhizomes or leaves to aboveground structures throughout the growing season.

Leaf tissue quality

Long-term herbivory at Whipple Field decreased leaf tissue quality (i.e., higher C:N ratio). Such an effect could arise directly from preferential herbivory of clones with high N content. Previous research has shown that goldenrod herbivores, and in particular *T. virgata*, can discriminate against clones of lower leaf quality (Brown and Weis 1995; Herzig 1995; Herzig and Root 1996).

The quality of leaf tissue, however, did not change among successional stages suggesting that other processes (e.g., pH) might be controlling the quality of leaf tissue over the course of succession. This is interesting given the fact that fertilization did increase the amount of ammonium available in the soil. Perhaps insect herbivores, by increasing the amount of recalcitrant litter, increase immobilization sufficiently to prevent the enrichment of fields by accumulated organic matter.

Insect performance

Although the feeding trials using plants from Whipple Field support the idea that the quality of leaf tissue has some effect on the growth of *T. virgata* larvae, *T. virgata* adult females were either absent or had reduced fecundity in late successional fields. The quality of leaf tissue in these fields was not different from early and mid successional sites where *T. virgata* produced a higher number of eggs/clutch. Although it is possible that other measurements of nutritional quality in goldenrods (e.g., defensive chemistry) could explain the patterns of *T. virgata* fecundity in both the successional sequence and Whipple Field, it also seems feasible that changes in a combination of factors (e.g., microclimate, predation) over the course of succession could account for the observed pattern.

Nitrogen cycling

In the long-term, herbivore exclusion increased goldenrod leaf N, total soil N, and N (ammonium) availability at Whipple field. Higher N inputs into the soil from goldenrod leaf litter could result in faster N cycling in the soil. Previous research at this site has shown faster leaf litter decomposition in sprayed plots (Carson and Root, in press). This result is consistent with the idea that faster N cycling should result in greater N accumulation in soils (Vitousek and Howarth 1991; Pastor et al. 1993). Flower production was also dramatically impacted by herbivores. Rapid decomposition of flowers of high N content might be crucial in terms of the overall budget of the plant, and the feedback between goldenrods and N cycling. Previous research has shown that flower litter can have dramatic impacts on nutrient dynamics (Zagt 1997).

Conclusions

Herbivores affect goldenrod allocation to sexual reproduction in the short term. The plasticity of the response of goldenrod to herbivore stress may hinge on the level of available resources: plants growing in resource-limited environments may be unable to allocate additional resources to flower production, while those growing in resource-rich environments can compensate for resources lost to herbivores.

Chronic herbivory might reduce the availability and quality of leaf tissue, and herbivore fitness and abundance in poor-quality sites. Previous research has shown that *T. virgata* larvae abandon patches of goldenrod with heavy herbivore damage in favor of those left intact (Herzig 1995; Herzig and Root 1996). The reduction in leaf tissue quality with chronic herbivory could account for this behavior.

This research adds to the body of literature demonstrating that in the long term, herbivores can decrease the quality of leaf litter and soil N availability (Pastor et al. 1993; Ritchie et al. 1998). Furthermore, these long-term effects appear to compensate for various short-term effects that increase N availability in the soil (e.g., added manure or frass, increased light penetration) (Pastor et al. 1993; Brown 1994).

Previous research has shown that preferential grazing of species with high leaf N content (e.g., legumes, hardwoods) relative to those with low N content (e.g., conifers) drives these reductions in leaf litter quality and soil N availability (Pastor et al. 1993; Ritchie et al. 1998); this study suggests that herbivores might decrease N availability and leaf litter quality by reducing the quality of leaf tissue *within the same plant species*. Future research will examine the mechanism by which these changes in leaf tissue quality occur.

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