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Trophic control across a natural productivity gradient with sap-feeding herbivores

Maria Uriarte and Oswald J. Schmitz

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Experiments examining the role that predators play in controlling herbivore damage to plant biomass are common in ecology. The interactive effect of productivity and predation on standing plant biomass in terrestrial ecosystems, however, remains poorly understood. Here we examine the role of predation and productivity on the damage sap-feeding herbivores inflict on goldenrod. Sap feeders are the dominant herbivores in this community. Sap is poor in nutrients and does not carry many of the chemical defense compounds of goldenrod. Sap-feeders should then be sensitive to changes in productivity and relatively impervious to the production of chemical defenses. We examined the effect of predation and fertilization on goldenrod across a productivity and successional gradient. We found that the effect of predators on controlling herbivore damage increased with increasing productivity. Some of these results are consistent with the Exploitation hypothesis proposed by Oksanen while others seem to reflect alternative mechanisms of trophic control across productivity gradients. Top-down control was strong in high productivity sites while plant competitive interactions may have obscured any pattern of top-down control in intermediate and low productivity sites.

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Many studies have examined the role predators play in food web dynamics (Sih et al. 1985, Brett and Goldman 1996, Polis and Winemiller 1996). This body of research indicates that there may be considerable variation in the influence top predators exert within and among field sites. An important challenge is to understand the source of this heterogeneity (sensu Hunter and Price 1992) in food web dynamics.

One potential source of heterogeneity recognized by early theory (Oksanen et al. 1981) is the net primary productivity of a location. According to this theory, the level of productivity determines the number of trophic levels that persist in a given system. For instance, systems of low productivity will have insufficient energy to support herbivores and consequently no predator effects should be observed. As productivity increases, enabling herbivore populations to gain a foothold in a system, we should see a correlated increase in the degree to which plants are limited by herbivore consumers (Oksanen et al. 1981). In highly productive environments carnivores persist, limiting herbivore populations and helping plants overcome strong limitation by herbivore consumers. Hence carnivores exert an indirect mutualistic effect on plants via top-down control of herbivore populations.

Despite the key role that Oksanen et al.'s (1981) exploitation hypothesis has played in shaping our thinking of trophic interactions, few studies describe how top-down effects change across space or time in three trophic level systems (but see Carpenter and Kitchell 1987, Hartvingtsen et al. 1995, Wardle et al. 1995). One determinant of productivity is the successional state of the field. In our study system, early successional fields have typically sustained agricultural

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exploitation, have low soil nutrient content, and exhibit low productivity. Productivity seems to increase with successional time. We used the natural changes in productivity across a successional gradient to examine the variation in trophic interactions. We studied the trophic interactions in goldenrod (*Solidago rugosa*) communities dominated by sap-feeding insects along a successional productivity gradient.

Oksanen's model assumes that (a) grazers move over a large area, and (b) grazers have high energy demands. Sap-feeders are immobile during their larval stage when they are most damaging to the plants and vulnerable to predation so they do not comply with the first assumption of the Exploitation hypothesis. However, their sedentary larvae and the poor nutritional quality of sap necessitate a fairly productive host and make them herbivores with "high energy demands" relative to the nitrogen available in the host. Host plants are more nitrogen rich in highly productive environments and thus more likely to meet the energy requirements of sap-feeders.

In summary, sap-feeders in our system meet some of the characteristics of grazers in Oksanen's model but not others. Our observed patterns of variation in trophic dynamics with productivity do not always support Oksanen et al.'s (1981) hypothesis suggesting alternative mechanisms of trophic control across productivity gradients for sap feeding herbivores.

Natural history

This study was conducted at the Yale-Myers Experimental Forest in Union, Connecticut, USA in old fields dominated by goldenrod (*Solidago rugosa*) but also inhabited by *Poa pratensis*, *Aster novaeangliae*, *Trifolium repens*, *Daucus carota* and *Phleum pratense*. Herbivorous insects include the generalist grasshopper *Melanoplus femurrubrum*, the grass specialist grasshopper *Chorthippus curtipennis*, the specialist goldenrod beetle *Trirhabda virgata*, the generalist sap-feeding spittlebug *Philaneus spumarius*, the sap-feeding plant bugs *Leptoterna dolobrata* (grass), *Lygus lineolaris* and *Lopidea media* (goldenrod). There are also assorted pentatomid bugs and various chrysomelid beetles. Predators include the jumping spiders *Phidippus rimator*, various small lycosids, i.e. *Schizocosa* sp., *Pirata* sp., the nursery web spider *Pisaurina mira*, and the crab spider *Misumena vatia*.

Goldenrod is a native, clonal rhizomatous perennial (Cronquist 1980, Werner et al. 1980) with a highly diverse insect fauna (> 100 species) (Root 1996). This plant is highly successful in disturbed environments, commonly dominating old fields throughout the Northeastern United States. Goldenrod fields provide an ideal system for studying trophic dynamics in successional time for two reasons. First, their successional trajectory is well documented (Lutz 1928, Bard 1952). Second, the natural history of many of the goldenrod insects has been studied (Messina 1978, Messina and Root 1980, McBrien et al. 1983, Abrahamson and McCrea 1986, McEvoy 1986, 1988, Cappuccino 1987, 1991, Abrahamson et al. 1988, Hamilton 1989, Root and Cappuccino 1992, Abrahamson and Weis 1996) and it is relatively simple to manipulate communities in the field.

There are linkages between the successional stage of a field, and the two variables that have been linked to trophic control mechanisms: its productivity and the documented trophic structure of the community. For example, changes in nutrient availability during succession can affect herbivore population dynamics. Studies on carbon and nitrogen cycling in some old-fields have shown that nitrogen availability may change during succession (Inouye et al. 1987, Tilman 1986, Zak et al. 1990). Increased nitrogen availability has a positive effect on the densities of some goldenrod herbivores (Meyer and Root 1996).

Both productivity and successional stage may also affect the light regime of a goldenrod stand and, as a consequence, the mechanisms of trophic dynamics including herbivore and predator behavior. Competition for light during succession affects the allocation of nitrogen to various parts of the plant. This allocation pattern affects the foraging behavior of both herbivores and predators. Research on goldenrod physiology indicates that leaf nitrogen concentration is proportional to light incidence (Hirose and Werger 1987, Schieving et al. 1992). Goldenrod tends to form dense monocultures in mid- and late-successional stages or at highly productive sites. As a result, light incidence to the middle and lower leaves of thick stands is low which cause nitrogen to concentrate in the canopy of the goldenrod stand. Foragers trying to optimize their nitrogen intake will most likely move to the higher parts of the plant as the clones get more dense, but foraging at the top of the plant is costly. Insects must travel higher than they would have to in sparse stands, shade may not be readily available, and vulnerability to predators may be greater (Loeffler 1992).

Methods

Experimental design

We conducted a series of experiments in three fields of increasing successional age: field 1 was plowed in 1995; field 2 was last cultivated in 1985; and field 3 in 1979. These fields represent early-, mid- and late-successional stages in this experiment. Field 3 had the highest productivity while field 2 had the lowest. Field 1 had surprisingly high plant biomass, perhaps owing to the competitive release created by plowing.

We used standard 0.1 m × 1 m tall exclosures made of aluminum screening (Belovsky 1986, Ritchie and Tilman 1992, Schmitz 1994) to create experimental communities at each of the three fields in mid-June. The exclosures were placed randomly in all three fields. We stocked the exclosures with one of the following treatments: (1) no insects ("Control"), (2) herbivores alone ("Herbivores") and (3) both herbivores and predators ("Predators"). Each treatment was replicated 10 times. If top-down control was occurring via a trophic cascade, then according to classical theory (Hairston et al. 1960, Oksanen et al. 1981) we expected that Herbivore plots would contain less plant biomass than Control plots because of the damage that herbivores inflicted on the plants. We also expected that in Predator plots, predators would release some of the pressure of herbivores on plants by reducing herbivore density, resulting in higher plant biomass than in Herbivore plots.

The experimental cages were stocked at the densities that the herbivores and predators were found in field surveys. Before stocking, we sampled the three fields using independent sweepnet surveys and determined the densities of herbivores and predators for each site. In these surveys, fields were sampled in the morning and in the late afternoon because insects are most active at this time. We swept 30 times over a 0.5-m^2 area at random locations in each of the three fields. We conducted surveys throughout the summer, at least twice a week. No effort was made to homogenize insect densities across fields because our intent was to determine the natural variability in productivity and trophic dynamic effects arising from existing field conditions. Insects that were present in more than 50% of the survey samples were stocked in each of the cages at their normal field densities. Table 1 lists the species that were used to stock exclosures in each of the fields and provides the absolute and relative abundances at which they were found in each field.

In addition to the 10 replicates of each treatment in each field, we fertilized a second set of replicates of Control exclosures (plants only) with 20:20:20 NPK at 10 g m^{-2} yr^{-1}. This level of fertilization increases the productivity of the field and does not have direct negative effects on plant tissue (Schmitz 1997). This set of exclosures was used to determine the degree of resource limitation on plants. We expected that those plots treated with fertilizer would have higher biomass than those left untreated and that this increase in biomass would reflect the degree of nutrient limitation of the field. The more productivity limits a site, the more its biomass will increase when provided with additional nutrients in the form of fertilizer.

All control cages were sprayed with a pyrethroid insecticide every two weeks to eliminate insect larvae emerging from eggs from previous years. This insecticide has no effect on goldenrod growth (Root 1996), does not bioaccumulate in animals or plants (Onkawa et al. 1980, Mumtaz and Menzer 1986, Louda and Rodman 1996), is rapidly degraded (Miyamota and Mikami 1983) and is not phytotoxic (Jones et al. 1986).

Trophic interactions change with the developmental stage of insects and plant phenology (Belovsky and Slade 1993, Schmitz 1997). Insect emergence at our site is concentrated at two time periods: early insects emerge in late May or early June while late insects emerge in July. To reflect these two emergence periods, the experiments were stocked twice: once at the beginning of the season, in early June and again in late July when the late summer herbivores started to emerge. Insects in exclosures were counted at regular intervals to ensure that herbivore and predator numbers matched densities in the fields. Many of the insects used to stock the cages early in the season declined in abundance or died later in the summer. We conducted weekly field surveys throughout the experiment to monitor how the abundance of various insects changed throughout the summer.

The plants in each cage were harvested in late September after the goldenrod had flowered. Non-goldenrod plants were clipped to ground level. Goldenrod plants were dug out of the soil to include roots and rhizomes. Goldenrod belowground structures, shoots, leaves and flowers were separated while all non-golden-

Table 1. Number of individuals of each arthropod species and relative abundances (in parentheses) stocked in exclosures in early (1), medium (2), and late (3) successional fields. Densities were obtained by repeated sweep net samples within each field.

Insects stocked in early summer	Field 1	Field 2	Field3
Leaf chewers			
Trirhabda larvae	0 (0)	0 (0)	2 (12%)
Lepidoptera caterpillar	0 (0)	1 (0.9%)	1 (0.6%)
Phloem-feeders			
Leptoterna dolobrata	1 (14%)	2 (18%)	4 (23%)
Adelphocoris sp.	1 (14%)	2 (18%)	4 (23%)
Leafhoppers	3 (43%)	3 (27%)	3 (17%)
Xylem-feeders			
Philaneus spumarius (nymphs)	2 (29%)	3 (27%)	3 (18%)
Predators			
Orb weaver	0	1	1
Salticid spider	1	2	1
Insects stocked in late summer	**Field 1**	**Field 2**	**Field 3**
Leaf chewers			
Melanoplus femurrubrum	1 (14%)	2 (22%)	0 (0)
Chorthippus curtipennis	1 (14%)	0 (0)	0 (0)
Chrysomelidae	0 (0)	1 (11%)	1 (12%)
Phloem feeders			
Pentatomidae	1 (14%)	1 (11%)	0 (0)
Lopidea sp.	2 (28%)	2 (22%)	1 (12%)
Xylem-feeders			
Philaneus spumarius (adults)	2 (28%)	3 (33%)	4 (50%)
Predators			
Saltícidae spider	1	1	1

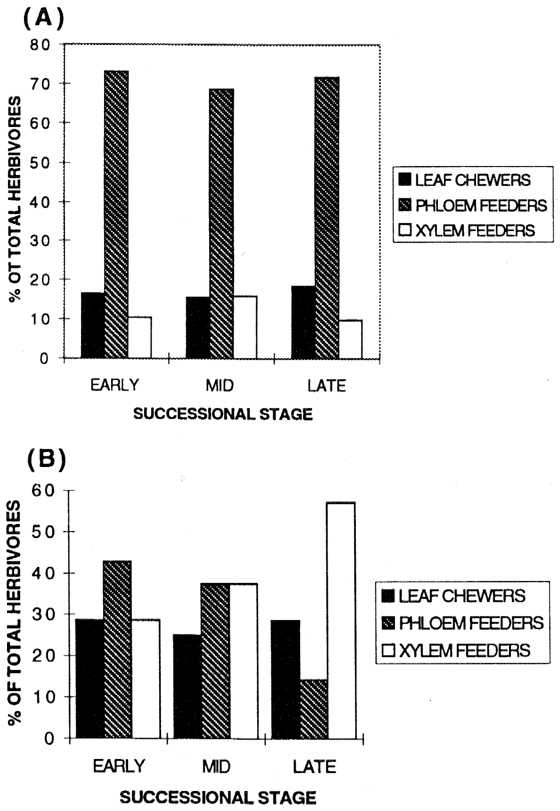

Fig. 1. Patterns of relative abundance of three feeding guilds in early, middle, and late successional fields dominated by goldenrod in early (A) and late summer (B).

rod plants were harvested and their biomass pooled together. All plant material was dried at 60°C for 48 h, then weighed.

Statistical analysis

Statistical analyses of all data were performed using SYSTAT for Windows version 5 (Wilkinson 1992). We used MANOVA to test for significance of fertilization and trophic structure on goldenrod shoot, flower and root biomass. We conducted planned comparisons between all possible pairs of Control, Herbivores and Predator treatments. We also compared differences in the biomass of all non-goldenrod plants, mostly grasses, included in the experimental plots. The biomass of non-goldenrod plants was pooled for this analysis.

Results

Patterns of herbivore abundance

The relative abundance of leaf-chewers, phloem-feeders and xylem-feeders changed throughout the summer (Fig. 1). *Philaneus spumarius*, a xylem-feeder, was the most abundant herbivore in the late successional field during late summer, although densities in the three fields were similar in early summer. Similarly, phloem-feeders (e.g. Miridae) became less abundant in the late field towards the end of the summer, although densities were similar in all three fields in July.

Effect of trophic structure on goldenrod biomass in unfertilized plots

According to the exploitation hypothesis, herbivores should decrease the biomass of naturally occurring vegetation in the absence of predators. Predators can indirectly increase vegetation biomass by reducing herbivore foraging and releasing pressure on vegetation. The strength of this effect should vary across productivity gradients. We compared the biomass of vegetation in Control, Herbivores, and Predator treatments to obtain a measure of the effect of trophic interactions on vegetation biomass.

Trophic structure had a significant effect on goldenrod shoot biomass in the middle and late successional fields but not in the early ones (Fig. 2A, Table 2). Herbivores significantly decreased goldenrod shoot biomass only in the late successional field. The effect of predators on herbivores significantly increased goldenrod shoot biomass both in the mid- and late-successional field. Flower biomass varied significantly in response to trophic structure in the mid-successional but not in the early or late fields (Fig. 2B, Table 2). In this case the introduction of predators significantly increased goldenrod flower biomass above the herbivore treatment. Belowground biomass did not significantly differ among trophic treatments for all three fields.

Effect of fertilization on goldenrod biomass

Fertilizer had a significant effect on goldenrod shoot biomass in the early and mid fields (Fig. 3A, Table 2), but not in the late-successional field. Flower biomass did not respond to fertilization in any of the fields (Table 2), and the response of belowground biomass was significant in the mid-successional field only (Fig. 3B, Table 2).

Other plant biomass

The biomass of non-goldenrod plants in the plots was not significantly affected by trophic structure or fertilization (Fig. 2C, 3C). Other plant biomass varied from 8% in the late-successional site to 45% in the mid-successional field. Non-goldenrod vegetation included both grasses and other forbs.

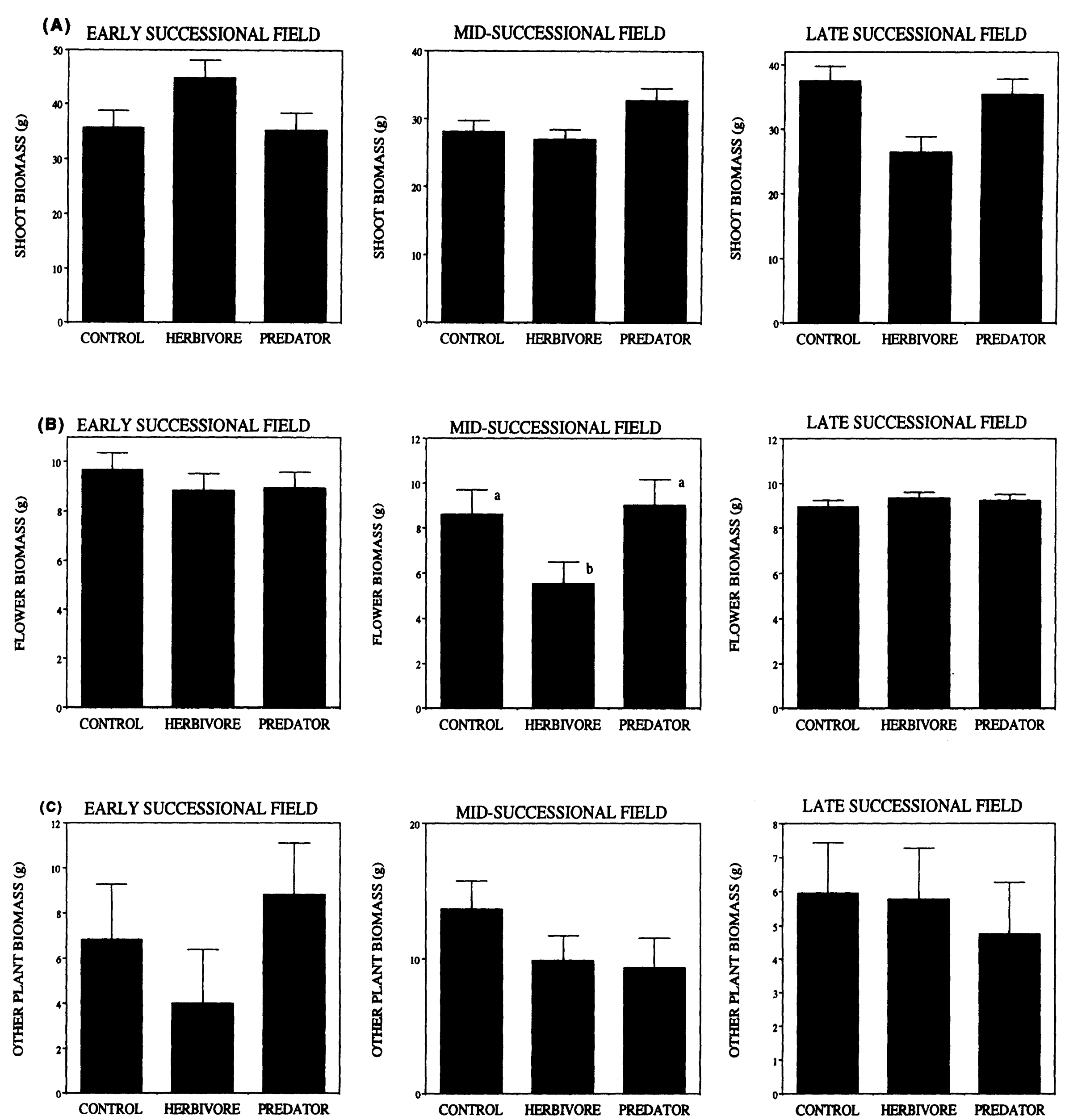

Fig. 2. Effect of trophic structure on *S. rugosa* shoot (A), flower (B), and (C) non-goldenrod plant biomass. Means and standard errors in early, middle, and late successional fields are presented. Different letters denote statistically significant differences (ANOVA, $p < 0.05$).

Discussion

Classical food chain theory (Oksanen et al. 1981) predicts a straightforward relationship between productivity and the existence of top-down control via a trophic cascade. However, there is certain skepticism that top-down control will occur in natural terrestrial systems because of the heterogenous range of factors that likely mitigate the strong consumer-resource interactions required to produce trophic cascades (Strong 1992, Polis and Strong 1996). We observed top-down control, manifest as a tropic cascade in goldenrod shoot biomass, in our experimental system but only in the late-successional field. Our results indicate that the likelihood for trophic cascades is dependent on factors in addition to productivity including resource availability, plant competition and plant diversity, which influence insect abundance and predator-prey interactions.

We found differences in the relative abundance of phloem- and xylem-feeding guilds among fields of different successional age. This can be explained by differences in productivity between fields. Fertilization data

Table 2. Summary effects of fertilizer, herbivory, and predation on herbivores on plant biomass (g) in early, middle, and late successional fields. Data are separated into flower, shoot and belowground biomass for *Solidago rugosa*. Non-goldenrod plants are clumped into one measure.

Dependent variable	Response variables											
	S. rugosa shoot			*S. rugosa* flower			*S. rugosa* belowground			Non-goldenrod plants		
Early-successional field	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*
Trophic structure		NS			NS			NS			NS	
Herbivore-Control		NS			NS			NS			NS	
Predator-Herbivore		NS			NS			NS			NS	
Fertilization	9.76	1,17	0.006		NS			NS			NS	
Mid-successional field												
Trophic structure	3.45	2,29	0.045	3.44	2,29	0.046		NS			NS	
Herbivore-Control		NS			NS			NS			NS	
Predator-Herbivore	6.58	1,20	0.018	4.94	1,20	0.037		NS			NS	
Fertilization	103.27	1,18	0.0001		NS		4.19	1,18	0.0192		NS	
Late-successional field												
Trophic structure	6.11	2,27	0.00647		NS			NS			NS	
Herbivore-Control	11.94	1,18	0.00028		NS			NS			NS	
Predator-Herbivore	7.87	1,18	0.011		NS			NS			NS	
Fertilization		NS			NS			NS			NS	

show mineral nutrients limit plants in the late field much less than in the younger-aged fields (Tilman 1986). As a result plants in late-successional fields are likely to be of higher nutritional quality. High plant nutritional quality has implications for the patterns of herbivore abundance. For example, xylem-feeders have the highest daily consumption rates of any herbivores: 100–1000 times their body weight (Mattson 1980). Xylem, however, is very low in nitrogen ($<0.01\%$) and xylem-feeders require large quantities of plant material. A highly productive environment may be able to support a higher density of xylem-feeders such as spittlebugs than a low productivity site. Higher densities of xylem-feeders may result in a decrease in the number of phloem-feeders (Maddox and Root 1990). In our experiment we found evidence that xylem-feeders were most abundant at highly productive sites.

The impact of predators also may have manifest themselves in different ways in different fields. In early-successional plots, neither the introduction of herbivores nor the introduction of predators changed goldenrod shoot biomass. Insects stocked in early successional cages were generalist herbivores that may have preferred grasses over forbs, particularly in the presence of predators. In mid-successional stages predators increased goldenrod shoot biomass with respect to herbivore-only cages and herbivores had no effect on goldenrod shoot biomass. Herbivores, however, did decrease other plant biomass in both herbivore only and herbivore-predator treatments in the mid-successional fields. This suggests that the pattern of plant abundance with trophic manipulation in this field arose from herbivore-mediated goldenrod–non-goldenrod plant interactions. Non-goldenrod forbs in this field accounted for 45% of the total plant biomass. Herbivores at this site are generalist or may have preferred other plants over goldenrod. In late-successional field, the introduction of predators released herbivore pressure on goldenrod shoot biomass. Spittlebugs accounted for a large proportion of the herbivores at this site; they are known to have a strong effect on goldenrod relative growth and photosynthetic rate (Meyer and Whitlow 1992, Meyer and Root 1993).

It is also possible that in the presence of predators, herbivores avoid moving up to the canopy of the goldenrod stand where they can bask in the sun and develop and feed more efficiently. Consequently, the risk of predation drives them to starvation. The vegetation at the late-successional site was dense and the insect environment more shaded. A shaded understory decreases the ability of insects to move to other plants without increasing their metabolic demands. Other research has shown that the risk of predation can affect the foraging behavior of herbivorous insects and limit movement in the top of plants (Porter 1982, Loeffler 1992, Beckerman et al. 1997, Schmitz et al. 1997). Spiders, the experimental predators, are vulnerable to desiccation and tolerant of shaded environments. Hence spider predators would have an advantage in late-successional sites, and the predation effect on herbivore plant consumption would be stronger at these sites.

The effect of trophic structure on flower biomass in the mid-successional field can be explained by the particular nutrient limitations specific to flowering. Flower production requires translocation of K to the inflorescence (Abrahamson and McCrea 1986). This field was the one that increased biomass most when fertilized (almost 100% increase), demonstrating strong nutrient

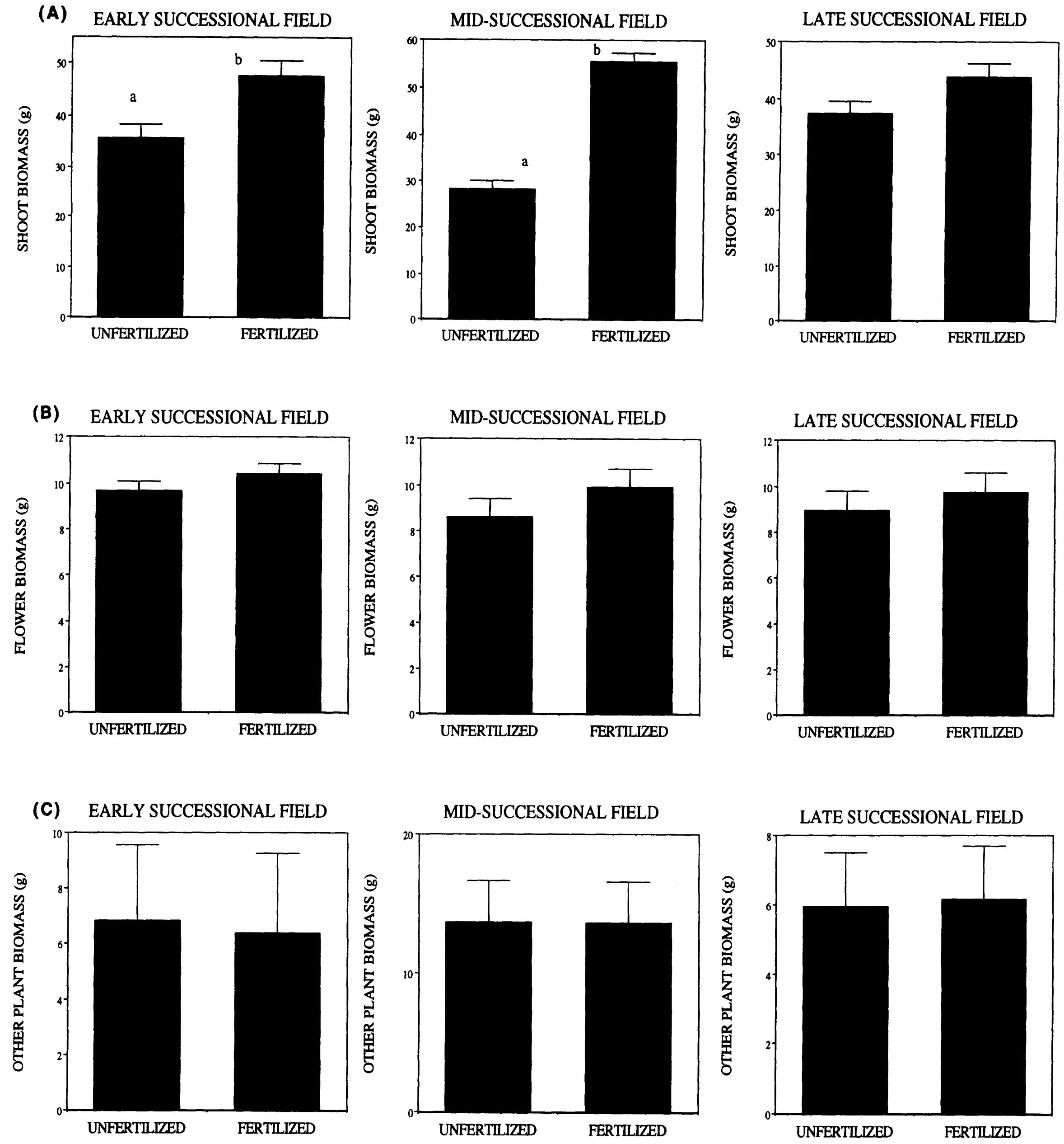

Fig. 3. Effect of fertilization on *S. rugosa* shoot (a), root (b), and (c) non-goldenrod plant biomass. Means and standard errors in early, middle, and late successional fields are presented. Different letters denote statistically significant differences (ANOVA, $p < 0.05$).

limitation. If the plants must live in a resource poor environment they might be forced to lower flower production when faced with the added stress of herbivory. This field was also rich in the forbs *Aster novaeangliae* and *Daucus carota* with flowering phenologies that parallel that of goldenrod. The added effect of competition between plants for resources at flowering time might have created the patterns we observed in flower phenology with trophic structure.

The effect of fertilization on goldenrod shoot biomass increased from the early- to the mid-successional field and then decreased in the late-successional field. These results are not surprising when one considers the nature of the disturbance introduced to create a successional gradient. The early-successional field was plowed in 1995, but had not been used for agriculture in the last 15 years. Typically early-successional fields in this area are colonized after many years of agricultural use; thus soil resources are depleted. This was not the case in this study. Furthermore, many of the goldenrod plants in the early successional plots grew from rhizomes that had remained viable after plowing and did not represent true early-successional goldenrod. This pattern of succession only represents recovery from agricultural disturbance and might nor accurately represent recovery from other disturbances, such as fire.

The positive effect of fertilization on belowground biomass in the mid-successional field suggests that additional resources may improve goldenrod asexual reproduction. Goldenrod establishment from seed in a field of this age is rare (Werner et al. 1980). It seems plausible that additional resources are used for asexual reproduction and not for flower production. The observed flower production (Fig. 2B) in herbivore plots corroborates this logic. The lack of fertilizer effects on belowground biomass in any of the other fields, on flower biomass in all fields, and the strong fertilizer response in shoot biomass in the middle field all suggest that nutrient limitation is strongest in the mid-successional field. Nutrient limitation might be highest at this site as a result of competition between plants in a highly diverse community.

Some of our results align with the theory of Oksanen et al. (1981) about the effect of productivity on the type of trophic control exhibited by a system. This hypothesis holds that "the more an ecological unit is limited by predation, the less its standing crop can respond to an increased productivity of resources". Our results support the converse of this statement: the more an ecological unit is limited by resources, the less its standing crop is likely to respond to predation on herbivores. Herbivory had its strongest effect in those fields in which goldenrod was not limited by resources because herbivores had a strong impact on goldenrod biomass that was released with the introduction of predators. The exploitation hypothesis, however, does not account for some of the patterns encountered in the mid-successional fields. Here the nutrient competition effect between plant species may override the effects of trophic structure. Also, predator-prey interactions may involve behavioral shifts by prey, interactions that are not accounted for by classical theory.

We suggest that theories that simultaneously account for trophic structure, changes in plant diversity with succession, resource availability, and competition between plants for the resources might prove fruitful in predicting the mechanisms of trophic control across successional productivity gradients (see also Polis and Strong 1996).

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