EXTENDING THE RESOURCE CONCENTRATION HYPOTHESIS TO PLANT COMMUNITIES: EFFECTS OF LITTER AND HERBIVORES

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Abstract. We extend the resource concentration hypothesis (herbivorous insects are more likely to find and stay in more dense and less diverse patches of their host plants) to plant communities. Specifically, whenever superior plant competitors spread to form dense stands, they will be found and attacked by their specialist insect enemies. This will decrease host plant abundance, causing a reduction in standing crop biomass, which will indirectly increase subordinate competitors and plant species richness. In this study, we found that a native, specialist chrysomelid beetle (Trirhabda virgata) in an old-field community decreased total standing crop biomass, leading to an increase in plant species richness. This reduction in biomass was due solely to a reduction in the biomass of the beetle’s host plant, meadow goldenrod (Solidago altissima), which was the dominant plant species in this community. Our results demonstrate that when a superior competitor increases in density, the per-stem impact of herbivores increases due to a buildup of these herbivores in high-density host patches. Specifically, we found that as goldenrod density increased, the per-stem abundance of Trirhabda virgata also increased. In turn, species richness increased as the negative effect of insects on goldenrod biomass increased.

Recent research suggests that litter accumulation could negate or cancel the effect of herbivorous insects on plant communities because litter accumulation increases with standing crop biomass, causing a decline in species richness. The litter accumulation hypothesis states that, in productive communities, the increase in the abundance of the superior competitor will lead to a dense accumulation of plant litter, causing a decline in species richness. Consistent with this hypothesis, we found that as the biomass of the dominant plant species increased, litter mass also increased. In turn, species richness decreased as the negative effects of litter on stem density increased. Interestingly, the effect of litter on stem density depended on whether insects were present. Our results suggest the potential for a general rule: specialist insect herbivores will function as classic keystone species in plant communities whenever host species form large, dense aggregations if host plants are dominant species.

Key words: goldenrod; herbivory; insects; litter; old-field community; resource concentration hypothesis; Solidago altissima; Trirhabda virgata.

INTRODUCTION

Examples of herbivorous insects regulating terrestrial plant communities are scarce, possibly because predators and parasites usually keep insect abundance low, or because plants are well defended, or both (Strong et al. 1984, Strong 1992, Hairston and Hairston 1993, Schmitz 1994, Carter and Rypstra 1995, Polis and Strong 1996, Price 1997, Uriarte and Schmitz 1998). Polis and Strong (1996) argued that the reticulate and diffuse nature of terrestrial food webs weaken trophic links and typically prevent strong top-down ef-

fcts of herbivorous insects on plant communities. Unfortunately, few empirical data directly test this assertion (Crawley 1997). Recent evidence suggests that there are at least three conditions that strengthen the links between insects and plants. These conditions frequently occur during outbreaks (Carson and Root 2000), whenever insects can muster an effective anti-predator defense (Carson and Root 1999), and potentially when there are strong feedbacks between host plant density and per-stem rates of damage by insects (Root 1973, Andow 1991, Carson and Root 2000).

The resource concentration hypothesis (Root 1973) describes a viable insect–plant feedback mechanism that may typically operate in plant communities. To date, this mechanism has not been applied at the scale of entire plant communities. The resource concentration hypothesis states that “herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands” (Root 1973). Numerous population-level studies lend strong support to this hypothe-
The resource concentration model and the litter accumulation hypothesis make contrasting predictions. The resource concentration model predicts that an increase in host plant density leads to an increase in specialist insect herbivores and a subsequent decrease in host plant biomass. Insects indirectly increase plant species richness by reducing host plant biomass if the host plant is a dominant competitor. The litter accumulation hypothesis predicts that plant litter accumulation causes a decrease in total stem density, leading to a decrease in species richness.

Litter accumulation, however, can have the opposite effect of herbivorous insects in plant communities. Increases in plant community biomass are often associated with higher levels of litter accumulation (Carson and Barrett 1988, Tilman 1993, Foster and Gross 1997), and a heavy accumulation of litter typically reduces species richness (Carson and Peterson 1990, Foster and Gross 1997, 1998, Carson and Root 2000). Although all species present contribute to litter accumulation, the dominant plant should contribute more to litter accumulation than do other species in old fields. We therefore tested the litter accumulation hypothesis, which states that, in productive communities, an increase in the abundance of the superior competitor will lead to a dense accumulation of plant litter, causing a decline in species richness (Fig. 1; Carson and Peterson 1990, Foster 1999, Suding and Goldberg 1999).

We conducted a four-year insect and litter removal experiment in a goldenrod-dominated old field in central New York to understand relationships among insect herbivory, litter accumulation, and plant communities. The goldenrod *Solidago altissima* is the dominant competitor in numerous old fields throughout the northeastern United States (Bazazz 1996). This species often forms dense, nearly monospecific stands with correspondingly high net primary production and standing crop biomass (Carson and Barrett 1988, Bazazz 1996, Carson and Root 2000); these stands result in communities of low diversity (Bazazz 1996, Carson and Root 2000). We tested if the density of the dominant plant species determined the abundance of herbivorous insects and their effect on plant diversity. We also tested whether dominant or subordinate plants primarily determined litter mass and the effects of litter on plant species richness. The factorial design of the experiment allowed us to integrate insect and litter effects.

**Methods**

**Study site**

We conducted this experiment in an abandoned agricultural field near Ithaca, New York, USA, (42°25' N, 76°31' W). The climate is humid continental, with mean annual rainfall of 880 mm, relatively uniform precipitation throughout the year, and an average frost-free growing season 146 d long from early May to early October (Neeley 1961).

The field was sprayed twice with an herbicide (Roundup, Monsanto Corporation, St. Louis, Missouri, USA) once in September and once in October of 1988, and plowed and disked in November. A small number of perennials survived this preparation and were killed with hand applications of the herbicide in the following spring. Consequently, this experiment started in the first year of old-field succession, from bare ground with species that established primarily from seed.
Natural history of old fields

The use of old fields as a model system has greatly contributed to our understanding of many ecological questions (e.g., Tilman 1982, Goldberg and Barton 1992, Bazzaz 1996). Goldenrods typically dominate old fields throughout the eastern and midwestern United States early in succession, and can persist as dominant species for decades (Mellinger and McNaughton 1975, Werner et al. 1980, Carson and Barrett 1988, Vankat and Snyder 1991, Bazzaz 1996). Herbivorous insects have been shown to reduce the growth and reproduction of goldenrod species (McCrea et al. 1985, Cain et al. 1991, Meyer 1993, Meyer and Root 1993, Brown 1994, Root 1996, Carson and Root 1999, 2000), and goldenrods typically suffer more damage than other old-field plant species (Root 1996, Carson and Root 1999, 2000). This study focuses on meadow goldenrod, Solidago altissima (or S. canadensis; see Kartesz 1994), a widespread, perennial, native, herbaceous species that supports 42 insect species with immature stages that specialize on goldenrod (Werner et al. 1980, Root and Cappuccino 1992). Two of these insects (Tri-rhabda virgata and Microrhopala vittata) are specialist chrysomelid beetles that are known to outbreak and periodically reach high abundance (Root and Cappuccino 1992).

Relationship to previous research

This study differed from the related, previous work of Carson and Root (1999) because it focused on a goldenrod specialist (the leaf-feeding insect Trirhabda virgata), rather than a generalist herbivorous insect (Philaenus spumarius). Also, vegetation was sampled in the fourth, rather than the third, year of succession (as in Carson and Root 1999). Carson and Root (2000) examined the long-term effects (over 10 yr) of insect removal on midsuccessional old fields. Here we examined effects during the establishment phase of succession, specifically the first four years of succession. By using methodologies similar to these studies, yet varying year, age of field, and the dominant herbivorous insect, we hoped that our results would lead to the most robust, general conclusions.

Design

Insecticide application.—The experiment used a two-factor split-plot design with two levels of insect abundance (present or removed) as the main plots and two levels of litter (present or removed) as the subplots (Fig. 2). We divided the field into 20 5 x 5 m main plots, arranged in 5 x 4 array and separated by 2-m buffer strips. We randomly selected one plot from pairs of adjacent main plots for application of the insecticide Fenvalerate. Fenvalerate is a broad-spectrum synthetic pyrethroid insecticide with no substantive side effects on the plants (for extensive details regarding the use of this pesticide, see Root [1996] and Carson and Root [2000]). We mixed Fenvalerate with water and sprayed it on the 10 randomly chosen plots at the recommended concentration of 300 g Fenvalerate/ha (Root 1996). We sprayed only during calm periods early in the morning or late in the evening (to avoid pesticide drift) at 2-wk intervals from late April to mid-September through the first four years of succession. We sprayed the untreated control plots with an equivalent amount of water. This application rate significantly reduced both insect herbivore loads and levels of insect plant damage on the common forbs and grasses (Root 1996, Carson and Root 1999, 2000). In the untreated control plots, substantial insect damage was found only on S. altissima and two uncommon understory forbs (Carson and Root 1999).

Litter.—We manipulated litter in three 1 x 1 m subplots haphazardly nested within each of the 5 x 5 m main plots. We had three types of litter treatments: litter removal, procedural control, and an unmanipulated control. We removed all litter in the litter removal subplots by hand in early spring without disturbing the...
soil surface. In the procedural control subplots, we removed and then replaced all litter to determine if our procedure for removing the litter had any additional influence beyond the intended effects of removing litter. The control subplots were left undisturbed. We removed litter on 16–18 April 1990, 7–9 April 1991, and 10–12 April 1992. We did not remove litter in the spring of 1989 because success was starting from tilled soil devoid of litter.

**Measurements of herbivore abundance.**—We quantified damage on 10 common old-field plant species during the first three years of this study and also visually surveyed the unsprayed control plots for damage on locally rare species (Carson and Root 1999). Our damage surveys uncovered extensive damage on two locally uncommon (<1% of total biomass) forbs (Plantago major and Rumex crispus); however, we never found damage >3% on any common species other than on the dominant species, *S. altissima*. Thus, we censused herbivorous insects on *S. altissima*, in plots without insecticide in early June 1992, because only this species was subject to heavy attack (for similar results in two other nearby old fields, see Carson and Root 1999). Herbivore loads measured in June are a reliable indicator of the degree of damage experienced by plants over the season because loads in spring are typically higher than in the summer (Root 1996). Our sampling method is explained and justified in detail elsewhere (Root and Cappuccino 1992, Root 1996) and here is reviewed briefly. The exact timing of the insect census was linked to insect phenology, and occurred in each year soon after the larvae of the chrysomelid beetle *Trirhabda virgata* (a dominant herbivore that specializes on goldenrod) molted into the third instar. We selected five goldenrod stems in each insecticide-sprayed plot and eight goldenrod stems in each control by haphazardly pointing a meter stick to the ground while looking away and then locating the stem nearest the base of the meter stick. We then carefully searched each stem for herbivores and measured stem length.

**Vegetation sampling**

We sampled total aboveground plant biomass in one randomly selected 0.125 m² circular quadrat in each subplot during the summer of 1992, four years after the start of the manipulations. Species richness was calculated as the number of species present in the biomass samples of each subplot. Samples of this size provided conclusive results in comparisons of biomass and species richness in several companion studies (Root 1996, Carson and Root 1999, 2000). Biomass samples were dried at ~80°C for 48 h and weighed to the nearest 0.1 g. In 1992, we measured stem density of all species in eight of the 10 pairs of main plots in randomly selected 20 × 20 cm sample plots placed ≥20 cm from the edge of each 1 × 1 m subplot. We also sampled the density of goldenrod in 1991 in randomly selected 1 × 1 m quadrats. For all statistical analyses, we used the density of goldenrod in 1991, rather than in 1992, because the specialist insects that typically attack this species in the spring of any given year (e.g., *Trirhabda* beetles) were oviposited on these goldenrods in the fall of the previous year and overwinter as eggs at the base of their host (Herzig 1995, Herzig and Root 1996). Thus, these beetles were responding to the 1991 density of these goldenrods, not their density in 1992.

**Statistical analyses and tests of hypotheses**

Species richness and abundance.—We tested for overall effects of insect suppression, litter manipulation (unmanipulated control, procedural control, removed), and their interaction on five response variables including plant species richness, total plant biomass, total plant density, and biomass and density of goldenrod with a split-plot ANOVA (PROC GLM in SAS/STAT v. 6.12; SAS Institute 1997). Insecticide treatment was completely randomized with respect to each pair of plots, and litter removal was nested within each plot.

**Testing predictions of the resource concentration model.**—We used linear regression to test if abundance of *Trirhabda* per stem in 1992 varied with goldenrod density in 1991 (the year when *Trirhabda* oviposited), as predicted by the resource concentration model. Insect abundance data and goldenrod densities were collected in unmanipulated control plots. We calculated the effect of herbivorous insects as an index, based on goldenrod biomass, for each of the 10 pairs of main plots:

\[
\text{Insect effect index} = \frac{(H' - L')}{\text{max of (H' - L' or H - L')}}
\]

where \(H'\) was the biomass of goldenrod in a subplot with herbivorous insects and unmanipulated litter (plus sign indicates presence), and \(L'\) was the biomass of goldenrod in the paired subplot without insects (i.e., insecticide-treated) and unmanipulated litter (sensu Wilson and Keddy 1986, Bonser and Reader 1995, Chase et al. 2000). Dividing by the maximum value of \(H' - L'\) constrained this index between 1 and −1, where 1 indicated complete facilitation (herbivory promotes the abundance of goldenrod), and −1 indicated complete inhibition (herbivory decreases the abundance of goldenrod). We performed the identical calculation for procedural control plots, substituting goldenrod biomass in procedural control plots for biomass in unmanipulated control. Thus, for procedural control plots, the insect effect index was the difference between goldenrod biomass in insecticide-sprayed and unsprayed procedural control plots, divided by the maximum of those two values.

We used linear regression to determine if inhibition of goldenrod by insects increased with increasing goldenrod density, as predicted by the resource concentration hypothesis. Separate analyses were performed for unmanipulated control and procedural control plots.
order to determine if the effect of herbivorous insects led to changes in species richness, we regressed species richness on the insect effect index. Separate analyses were performed for unmanipulated control and procedural control plots.

**Testing predictions of the litter accumulation hypothesis.**—The litter accumulation hypothesis states that litter mass increases with biomass of the dominant plant species, and the effects of litter on stem density and plant species richness should increase with litter mass. We used analyses of covariance (ANCOVA) to test if litter mass varied with dominant or subordinate plant biomass, and if insects affected either of these relationships. We used the presence or absence of insects as the categorical explanatory variable, and the continuous explanatory variable was either goldenrod biomass or subordinate plant biomass. Litter mass was the response variable. Separate analyses were performed for unmanipulated control and procedural control plots.

We calculated the effect of litter, as an index based on total stem density, to test if the effect of litter increased with litter mass. Because litter manipulations were nested within insecticide manipulations, we calculated the litter effect index for plots with and without herbivorous insects. By testing the effect with and without herbivorous insects, we could determine whether the litter effect was different when insects were present vs. when they were absent.

For plots with insects present,

\[ \text{litter effect index} = \frac{(H^+L^- - H^0L^-)}{\text{maximum of} (H^0L^- \text{ or } H^+L^-)} \]

and for insecticide-treated plots,

\[ \text{litter effect index} = \frac{(H^-L^+ - H^-L^-)}{\text{maximum of} (H^-L^+ \text{ or } H^0L^-)} \]

where \( H^0L^- \) and \( H^-L^- \) were defined as before; \( H^+L^- \) was total stem density in the subplot with insects and with litter removed; and \( H^-L^- \) was total stem density in the subplot without insects and unmanipulated litter (sensu Foster and Gross 1997, Suding and Goldberg 1999). Dividing by the maximum value of \( H^0L^- \) or \( H^-L^- \) constrained this index between 1 and –1, where 1 indicated complete facilitation (litter promotes total stem density), and –1 indicated complete inhibition (litter decreases total stem density). We also calculated this index for procedural control plots. This calculation is identical to the previous one, except that stem density in procedural control plots replaced stem density in unmanipulated litter plots. Density data was collected in only eight of the 10 main plots. Therefore, we calculated 16 indices based on unmanipulated litter control plots (eight for insecticide-treated plots and eight for insecticide-free control plots) and 16 indices based on procedural control plots (eight for insecticide-treated plots and eight for insecticide-free control plots).

\[
\text{Table 1. Mean (± 1 SE) litter mass removed in insecticide-sprayed and control plots in each year.}
\]

<table>
<thead>
<tr>
<th>Year</th>
<th>Spray</th>
<th>Control</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>247 ± 26.7</td>
<td>247 ± 24.6</td>
<td>0.34</td>
<td>0.97</td>
</tr>
<tr>
<td>1991</td>
<td>320.2 ± 26.8</td>
<td>223 ± 15.4</td>
<td>4.04</td>
<td>0.003</td>
</tr>
<tr>
<td>1992</td>
<td>375.7 ± 32.3</td>
<td>203.1 ± 13.8</td>
<td>5.20</td>
<td>0.0006</td>
</tr>
</tbody>
</table>

*Note:* We compared the means each year with a paired \( t \) test (df = 10; Bonferroni-adjusted critical value of \( P = 0.017 \)).

We used ANCOVA to determine if increased litter mass led to a greater inhibition of density, as measured by the litter effect index and the effects of insects. We used the presence or absence of insects as the categorical explanatory variable, litter mass as the continuous explanatory variable, and the litter effect index as the response variable. Separate analyses were performed for unmanipulated control and procedural control plots. We regressed species richness on the litter effect index to determine if the effect of litter led to changes in species richness. Separate analyses were performed for unmanipulated control and procedural control plots.

**RESULTS**

**Insect and litter abundance**

*Trirhabda virgata*, a chrysomelid beetle that specializes on goldenrods, was the dominant herbivore during the fourth year of succession (1992), accounting for >90% of the insects on goldenrod by abundance in the insecticide control plots. Abundance of *Trirhabda virgata* was \( 4.51 ± 1.31 \) individuals/stem in control plots. Damage surveys in control plots in a previous, related study demonstrated that insect damage >3% was restricted to *Solidago altissima* (Carson and Root 1999). The insecticide treatment was highly effective at reducing insect damage (see also Carson and Root 1999); indeed, we never found insects foraging on goldenrods in sprayed plots in our censuses. Litter mass did not differ between sprayed and control plots in the first year of removal, but was greater in sprayed plots than in plots with insects in the last two years of removal (Table 1).

**The influence of herbivory and litter on species richness and plant abundance**

Plant species richness, density, and biomass.—Litter and herbivorous insects had opposite effects on plant species richness. Litter significantly decreased plant species richness, whereas insect herbivory significantly increased richness by ~4–5 species (Fig. 3). Litter and herbivory affected richness independently (i.e., there was no significant interaction).

Litter accumulation significantly decreased total stem density, whereas herbivorous insects had no sig-
significant effect on total stem density (Fig. 4A). Litter accumulation still decreased total stem density when goldenrod density was removed from the analysis (Fig. 4B), and did not affect goldenrod stem density (Fig. 4C). This suggests that the reduction of stem density by litter had little to do with goldenrod density. The presence of litter increased aboveground plant biomass, whereas herbivorous insects significantly decreased total aboveground plant biomass (Fig. 5A). There was no significant interaction (Fig. 5A). The reduction of total aboveground plant biomass by insect herbivory was explained entirely by the reduction in goldenrod biomass (Fig. 5B). There was no significant effect of either litter removal or insect suppression when goldenrod biomass was removed from the analysis (Fig. 5B). Herbivory significantly decreased goldenrod biomass, but litter and the interaction between litter and insects did not significantly affect goldenrod biomass (Fig. 5C).

Testing the resource concentration model

Per-stem abundance of *Trirhabda* in 1992 increased with goldenrod density, as measured in 1991 (Fig. 6A). We also found that the per-stem percentage of leaf tissue damaged increased with increased goldenrod density in 1991 (Fig. 6B; for the methods used to estimate leaf damage, see Carson and Root [1999, 2000]).

The negative impact of insects on the biomass of goldenrod did not increase with goldenrod density in the unmanipulated litter control plots (Fig. 6C). However, the point in the top right corner of the figure was identified, statistically, as an outlier because its studentized residual exceeded the Bonferroni (alpha-splitting) correction critical value for determining outliers (Belsley et al. 1980, Kleinbaum et al. 1998). When this point was excluded from the analysis, the relationship between the effect of insects and goldenrod density was statistically significant ($F_{1,8} = 6.90, P = 0.03, r^2 = 0.46$). We have no biological reason to remove this point, and therefore do not exclude it from the analysis.

![Figure 3](image1.png)

**Fig. 3.** The influence of herbivorous insects and plant litter on mean (±1 SE) species richness. The presence of herbivorous insects increased species richness ($F_{1,9} = 9.89, P = 0.012$). The presence of plant litter decreased species richness ($F_{2,26} = 12.24, P < 0.0001$). There was no significant interaction between insects and litter ($F_{2,26} = 0.85, P = 0.437$).

![Figure 4](image2.png)

**Fig. 4.** (A) The influence of herbivorous insects and plant litter on mean (±1 SE) total stem density. Herbivorous insects did not affect total stem density ($F_{1,7} = 0.43, P = 0.535$). Plant litter decreased total stem density ($F_{2,28} = 18.87, P < 0.0001$). The interaction between insects and plant litter was marginally significant ($F_{2,28} = 2.51, P = 0.099$). (B) Comparison of mean stem density with goldenrod stems was not included. Removing goldenrod from the analysis did not change these results for insects ($F_{1,7} = 0.93, P = 0.367$) or litter ($F_{2,28} = 20.84, P < 0.0001$) but did change the significance of the interaction ($F_{2,28} = 2.37, P = 0.112$). (C) Goldenrod stem density was not affected by herbivorous insects, litter, or the interaction between insects and litter ($F_{1,8} = 0.82, P = 0.396$ for effects of insects; $F_{2,28} = 1.61, P = 0.218$ for effects of litter; $F_{2,28} = 1.65, P = 0.211$ for the interaction between insects and litter).
F I G . 5. (A) The influence of herbivorous insects and plant litter on mean (±1 SE) total aboveground plant biomass. Herbivorous insects decreased aboveground plant biomass ($F_{1,9} = 7.69, \, P = 0.022$). Plant litter marginally significantly increased aboveground plant biomass ($F_{2,36} = 2.95, \, P = 0.065$), and the interaction between insects and plant litter was not significant ($F_{2,36} = 0.16, \, P = 0.850$). (B) The influence of herbivorous insects and plant litter on mean total aboveground plant biomass without goldenrod biomass. There was no significant difference in biomass between plots with and without insects or litter when the goldenrod biomass was removed from the analysis ($F_{1,9} = 0.58, \, P = 0.466$ for insects; $F_{2,36} = 1.66, \, P = 0.205$ for litter; $F_{2,36} = 1.17, \, P = 0.322$ for the interaction). (C) The influence of herbivorous insects and plant litter on mean (±1 SE) aboveground goldenrod biomass. Herbivorous insects decreased aboveground goldenrod biomass ($F_{1,9} = 7.65, \, P = 0.022$). Removing litter did not affect aboveground goldenrod biomass ($F_{2,36} = 0.45, \, P = 0.638$), and the interaction between insects and plant litter was not significant ($F_{2,36} = 1.87, \, P = 0.169$).

Most importantly, species richness increased as the negative effect of insects on goldenrod became more severe in the unmanipulated litter control plots (Fig. 7A). Specifically, when the insect effect index was negative (inhibitive), species richness was much higher. There was no relationship between the insect effect index and species richness in the procedural control plots (Fig. 7B).

Testing the litter accumulation hypothesis

Litter mass was accidentally not recorded for one procedural control plot. Therefore, we did not include data from this plot in any analysis. Litter accumulation increased as goldenrod biomass increased in both unmanipulated litter control plots and procedural control plots, and insects did not affect these relationships (Fig. 8A, B). There was a marginally significant decrease in litter accumulation with subordinate plant biomass in litter control plots, and insects did not affect these relationships (Fig. 8C). Litter accumulation was not related to subordinate plant biomass or insects in procedural control plots (Fig. 8D). We predicted that the effect of litter on total stem density, measured as the litter effect index, would increase with litter mass, but we did not find this relationship in litter control plots (Fig. 9A). The litter effect index was significantly more negative (more inhibitive) in the absence of insects in litter control plots; this indicates that insects alleviated the effect of litter on stem density (Fig. 9A). We did find a significant relationship between the litter effect index and litter mass in procedural control plots, and this relationship depended on the presence or absence of insects (significant interaction; Fig. 9B). As in the litter control plots, insects independently alleviated the effect of litter on stem density (Fig. 9B). As predicted by the litter accumulation hypothesis, species richness decreased as the effect of litter became more inhibitory in both litter control and procedural control plots (Fig. 10).

DISCUSSION

The top-down effect of herbivorous insects

Herbivorous insects decreased total aboveground plant biomass and increased species richness in this 4-yr-old goldenrod-dominated old field. The decrease in total plant biomass was accounted for entirely by the decrease in goldenrod biomass. These results are similar to those in herbaceous communities in England (Henderson and Clements 1977, Brown et al. 1988, Brown and Gange 1989, 1992) and North America (McBrien et al. 1983, Carson and Root 1999, 2000), where herbivorous insects increased species richness because they disproportionately and negatively affected the dominant native plant species. This adds to a growing list of studies that document clear examples of top-down effects of herbivorous insects on reducing standing crop biomass (Henderson and Clements 1977, Chase 1998, Carson and Root 1999, 2000).
FIG. 6. (A) Per-stem abundance of *Trirhabda* in 1992 increased with goldenrod density measured in 1991 ($F_{1,9} = 6.90, P = 0.030, r^2 = 0.46$). (B) Per-stem percentage of leaf tissue damaged in 1992 showed a marginally significant increase with goldenrod density measured in 1991 ($F_{1,9} = 4.73, P = 0.07, r^2 = 0.40$). (C) Insect effects on goldenrod biomass did not increase with goldenrod density measured in 1991 ($F_{1,9} = 0.01, P = 0.915, r^2 < 0.01$). Insect effects were based on goldenrod biomass and were constrained between values of 1 and −1, with 1 indicating complete facilitation by insects and −1 indicating complete inhibition or consumption by insects (see Methods for details). The point in the upper right corner of the graph was statistically identified as an outlier. When this point was removed from the analyses, insect effects significantly increased with goldenrod density ($F_{1,8} = 6.90, P = 0.03, r^2 = 0.46$; see Results for further details).

These findings run counter to much theoretical and empirical work that suggests that factors such as predators and plant defenses limit top-down effects of herbivorous insects on terrestrial plant communities (Strong et al. 1984, Strong 1992, Hairston and Hairston 1993, Schmitz 1994, Carter and Rypstra 1995, Folis and Strong 1996, Price 1997, Uriate and Schmitz 1998). Strong (1992) argues that the reticulate trophic connections in terrestrial communities prevent runaway consumption and reduction of standing crop in terrestrial systems. Predators and plant defenses may limit the effect of herbivorous insects on plant communities, but may not always obviate top-down effects. We suggest that some conditions strengthen trophic links between insects and their host plants, and allow for top-down effects. We can identify at least three sets of conditions, none of which is mutually exclusive, and which may occur frequently: (1) during insect outbreaks, when outbreaks are common relative to the life

FIG. 7. Plant species richness increased as the effect of insects on goldenrod became more inhibitive in the litter control plots ($F_{1,9} = 4.88, P = 0.058, r^2 = 0.38$). Specifically, when the insect effect index was negative (inhibitive), species richness was much higher. This relationship was not observed in the procedural control plots ($F_{1,8} = 0.94, P = 0.361, r^2 = 0.10$). Effects of insects on goldenrod are as defined in Fig. 6C.
F I G . 8. (A) Litter mass increased with increasing goldenrod biomass in litter control plots ($F_{1,19} = 12.93, P = 0.002$), and this relationship was not affected by herbivorous insects ($F_{1,19} = 0.33, P = 0.573$). (B) Litter mass increased with increasing goldenrod biomass in procedural control plots ($F_{1,18} = 6.75, P = 0.019$), and this relationship was not affected by herbivorous insects ($F_{1,18} = 0.33, P = 0.573$). (C) Litter mass marginally significantly decreased with increasing subordinate plant biomass (total biomass without goldenrod biomass) in litter control plots ($F_{1,19} = 4.05, P = 0.060$), and this relationship was not affected by herbivorous insects ($F_{1,19} = 0.06, P = 0.805$). (D) Litter mass was not related to subordinate plant biomass in procedural control plots ($F_{1,18} = 0.00, P = 0.995$), and this relationship was not affected by herbivorous insects ($F_{1,18} = 0.00, P = 0.995$).

The resource concentration model of plant community regulation

The resource concentration model predicts that the per-stem abundance of herbivorous insects, and their subsequent effect on their host plant, should increase with host plant density. If the host plant is competitively dominant, then insects will have a top-down effect on species richness. In this study, we found that the per-stem abundance of the dominant herbivorous insect, *Trirhabda virgata*, and the percentage of leaf damage increased with goldenrod (*Solidago altissima*) density (Fig. 6B). The increase of this univoltine insect probably resulted from attraction to the high-density patches of goldenrod (sensu Morrow et al. 1989, Herzig and Root 1996). The increase in these beetles in high-density patches is not surprising because these beetles tend to preferentially colonize dense and undamaged patches of their host plants (Morrow et al. 1989, Herzig 1995, Herzig and Root 1996, Carson and Root 2000). Indeed, *Trirhabda* beetles can fly for many kilometers to colonize lush and undamaged goldenrods (Herzig and Root 1996).

We did not observe the predicted negative relationship between the impact of insects and goldenrod density (Fig. 6C). If we exclude the data point in the upper right corner of the graph, based on its statistical identification as an outlier, then the relationship between the effect of insects and goldenrod density becomes significant (see Results for further details). We have no biologically based reason to exclude this point. However, given that we found an increase in both *Trirhabda* and the damage that they caused with increasing goldenrod density, it would certainly not be surprising if they ultimately cause a concomitant decrease in den-
Fig. 9. (A) The litter effect index was not related to litter mass in litter control plots ($F_{1,15} = 0.01$, $P = 0.937$). Insects marginally significantly lessened the effect of litter on stem density in litter control plots ($F_{1,15} = 4.08$, $P = 0.065$). (B) The litter effect index was related to litter mass in procedural control plots ($F_{1,14} = 11.65$, $P = 0.005$). Insects lessened the effect of litter on stem density ($F_{1,14} = 11.97$, $P = 0.005$) and increased the slope of the relationship between the effect of litter and litter mass (significant insect $\times$ litter mass interaction, $F_{1,14} = 5.12$, $P = 0.045$). The litter effect index was based on total stem density and was constrained between values of 1 and $-1$, with a 1 indicating complete facilitation by litter and $-1$ indicating litter reduced stem density to 0 (see Methods for details). Filled circles indicate the litter effect in the presence of insects; open circles indicate litter effect in the absence of insects.

FIG. 10. (A) Plant species richness showed a marginally significant increase as the inhibitive effects of litter decreased in litter control plots ($F_{1,15} = 4.16$, $P = 0.060$, $r^2 = 0.23$). (B) Plant species richness significantly increased in procedural control plots ($F_{1,14} = 5.13$, $P = 0.041$, $r^2 = 0.28$).

The decrease in density may take some time to occur, however. Carson and Root (2000) found a two-year lag between declines in density and damage caused by a related specialist chrysomelid beetle (Microrhopala vittata). Goldenrod is a widespread, native perennial that is host to more than 40 specialist insects (Root and Cappucino 1992). Two of these, Trirhabda virgata and Microrhopala vittata, have now been shown to substantially reduce the biomass of this species, and both species cause greater damage in denser stands (McBrien et al. 1983, Carson and Root 2000). In a related study, Carson and Root (2000) also found a similar relationship between density and damage in a much older goldenrod-dominated old field a few kilometers away from the field considered in the present study. Overall, these responses suggest that this is a fairly robust result for goldenrod-dominated communities.

Interestingly, two data points suggest that insects had strong facilitation effects on goldenrod biomass (insect effect index $\equiv 1$; Fig. 6C). One of these points is the statistical outlier just discussed, and we have no biological explanation for this observation. The second occurred in a patch of low goldenrod density. The individuals of goldenrod in this patch experienced less damage by insects. The slight damage experienced by these goldenrods may have caused changes in allocation, or increased light availability to underlying leaves, allowing for compensatory growth (e.g., Belsky 1986).

Most importantly, as the negative influence of the beetles on goldenrod biomass increased, plant species richness...
richness increased in unmanipulated litter plots (Fig. 7A). The increase in plant species richness that resulted was probably caused by an increase in resources, particularly light, that were freed up by the reduction in the dominance and abundance of goldenrod (Carson and Pickett 1990, Brown 1994, Carson and Root 2000). Interestingly, there was no relationship between the effect of insects and species richness in procedural control (litter removed and replaced) plots (Fig. 7B), even though we did find that the presence of insects lowered species richness in the procedural control plots (Fig. 3). This may have occurred because *Trirhabda* over-winter as eggs in the litter layer (Herzig 1995). Disrupting, removing, and replacing litter prior to their emergence in the spring may have removed eggs from the plots as litter was excavated from the plot, placed outside the plot, and then replaced back into the plot. It is possible that the procedure itself may have caused egg mortality. Similarly, Facelli (1994) found that the presence of plant litter increased arthropod abundance, activity, and subsequent damage on tree seedlings. Clearly, more research is required to sort out the complex patterns by which litter, insects, and their interactions influence plant communities.

The resource concentration model explains how insects could commonly play a major role in regulating plant communities by causing greater damage when host plants that are superior competitors spread and become dominant. This regulation would only be “switched on” when dominant species become dense and are then found by their insect enemies. Without the mitigating influence of insects, these plant species would depress the abundance of, or exclude, subordinate plant species (sensu Carson and Root 2000). Regulation of plant communities by the resource concentration model could be a very general phenomenon. The per capita abundance of specialist herbivorous insects is often greater in monocultures than polycultures (e.g., Root 1973, Risch et al. 1983, Andow 1991, Coll and Bottrell 1994, Schellhorn and Sork 1997) and this increase in insect abundance can lead to an increase in per capita damage on host plants and reductions in plant vigor (Bach 1980, Andow 1991, Ramert and Ekbbom 1996, Carson and Root 2000). If native plants that are superior competitors are also widespread, which is typical, then these plants will have a substantially richer herbivorous insect fauna than inferior competitors that are sparsely distributed (Strong et al. 1984). Consequently, widespread, superior competitors may commonly have specialist insects that track their abundance, thereby reducing the impact of these dominant species on subordinate plant species within the community.

This begs the question of why dense patches of dominant host plants can persist for long periods of time without being decimated by herbivores (e.g., decades for goldenrod: Mellinger and McNaughton 1975, Werner et al. 1980, Carson and Barrett 1988, Vankat and Snyder 1991, Bazzaz 1996). A number of potential answers exist. First, smaller patches within a field, or individual clones, may indeed be decimated. Because of the time lag between increases in plant density and their discovery by insects, less dense patches may increase in density concomitant with the decimation of other patches. Thus, observation at the field scale may suggest persistence of the dominant plant. Second, host plants may become more resistant with subsequent attacks, or more resistant plants may spread. Third, it makes sense that if the herbivorous insects can track host plant density, eventually their predators should track their density. When this occurs, predators may prevent the decimation of host plant patches (Strong 1992). However, it is important to stress again that herbivorous insects need not decimate host plant populations to regulate plant communities (e.g., Brown et al. 1988, Brown and Gange 1989, 1992, Carson and Root 2000). Herbivorous insects need only reduce the competitive impact of dominant host plants on subordinate plants to allow coexistence of the subordinates.

Generalist vs. specialist herbivorous insects.—We suggest that keystone predation models based primarily on productivity (e.g., Armstrong 1979, Holt et al. 1994, Leibold 1996) may apply more to highly polyphagous species that may increase with net primary production (Ritchie 2000), whereas the resource concentration model may apply more to specialist insects that respond to host plant density. Generalist herbivores can respond to productivity. For example, Chase et al. (2000) found an increase in the effect of large mammalian herbivores on plant communities over a broad increase in productivity. Similarly, McNaughton et al. (1989) found that biomass of herbivores and consumption by herbivores increased with primary productivity. For insects, Carson and Root (1999) found that the highly polyphagous spittle bug (*Philaneus spumarious*) significantly reduced goldenrod abundance at this same Ithaca field site and two others, but there was no relationship between plant density and spittle bug abundance ($F_{1,9} = 1.44, P = 0.26, R^2 = 0.15$). As just outlined, monophagous insects respond to host plant density, and their effects on plant communities are better predicted by the resource concentration model. It is important to note that the resource concentration model and models based on productivity make similar predictions when the density of the host plant varies with productivity. This is probably a common phenomenon. Further research that separates effects of plant density vs. biomass (productivity) and effects of specialist herbivores vs. generalist herbivores is required.

Effects of litter accumulation

Similar to findings of other studies, we found that litter decreased species richness and total stem density (Carson and Peterson 1990, Facelli and Pickett 1991, Tilman 1993, Foster and Gross 1997, 1998, Foster
The litter accumulation hypothesis explains these results. That is, in productive communities, increases in the biomass of the superior competitor can lead to a dense accumulation of plant litter, causing a decline in species richness (Carson and Peterson 1990, Foster 1999, Suding and Goldberg 1999). In line with this hypothesis, we found that litter mass increased with the biomass of the dominant plant species (Fig. 8). Although insects can potentially increase litter accumulation by increasing abscission (Owen 1978, Risley and Crossley 1988), or decrease litter through consumption (Whittaker and Woodwell 1969), we found that insects had no effect on the relationship between goldenrod biomass and litter mass.

The litter accumulation hypothesis predicts that litter will inhibit stem density more with increasing litter mass. We did not find a consistent relationship between the litter effect index and litter mass. We found that insects, not litter mass, determined the litter effect index in control plots, whereas litter mass, insects, and their interaction determined the litter effect index in procedural control plots (Fig. 9B). As previously argued, the removal and replacement of litter in procedural control plots may have disturbed the overwintering Trirhabda virgata. This would have allowed the relationship between the litter effect index and litter mass. In the control plots, however, herbivorous insects may have obviated this relationship.

Increases in the biomass of goldenrod probably decreased richness in two ways: (1) by increasing litter mass and decreasing the establishment of other species, and (2) through competitive effects on the subordinate plants. This is similar to Foster (1999), who found that the negative effects of competition and litter on the establishment of two target species became more severe with increased total aboveground plant biomass. We found that litter mass increased with increasing biomass of goldenrod (Fig. 8) and with total aboveground plant biomass ($F_{1,18} = 20.86, P = 0.0002, R^2 = 0.54$), but was not related to aboveground plant biomass without the biomass of goldenrod (Fig. 5). This was surprising, given the high biomass of subordinate species in some plots. One explanation would be that litter from other species in these plots decomposes more quickly. However, we did not directly quantify the contributions that each species made to litter, nor did we quantify the relative rates of decomposition of each species. In the absence of this information, and because of the strength of the relationship between goldenrod and litter mass, we conclude that the dominant plant determined the litter mass in this study. Also similar to the results of Foster (1999), goldenrod probably decreased the establishment of other species through competition. Specifically, dense stands of goldenrod can dramatically decrease light levels reaching the soil surface, thereby reducing stem density and species richness (Carson and Pickett 1990, Bazzaz 1996, Carson and Root 2000).

Dense stands of goldenrod, therefore, can suppress richness both through competitive effects and by creating a dense litter layer. This suggests another feedback loop based on abundance of the dominant plant species. Specifically, goldenrod creates a litter layer that may prevent the establishment of other species, thereby decreasing competition. Additionally, litter may create better environmental conditions (i.e., increased soil moisture) for the already present goldenrod (Facelli and Pickett 1991). This competitive release and habitat amelioration can allow goldenrod to increase in size and abundance, which, in turn, may feed back into the litter layer when goldenrod senesces in the fall.

This positive feedback loop between the dominant plant and litter directly opposes the negative feedback loop between the dominant plant and specialist herbivorous insects. Herbivorous insects decrease the size and abundance of goldenrod. This decreases the contribution of goldenrod to litter and decreases the competitive displacement of other species by goldenrod. Indeed, we found that the presence of insects reduced the negative effects of litter on total stem density (Fig. 9). Herbivorous insects can thin stands of goldenrods by damaging leaves, killing stems, decreasing vegetative reproduction, disrupting belowground clonal integration, reducing nitrogen uptake, and reducing final plant size (McCrea et al. 1985, Cain et al. 1991, Brown 1994, Carson and Root 1999, 2000). Insects decreased goldenrod biomass, which probably increased light levels in stands of goldenrod (e.g., Brown 1994, Carson and Root 2000). Decreasing goldenrod biomass also decreased litter mass (Fig. 8). Thus, because the effects of litter depended on goldenrod biomass and insects determined goldenrod biomass, insects ultimately influenced the effects of litter accumulation.

Conclusions

We found that herbivorous insects increased species richness and decreased standing crop, largely through the effects of insects on the dominant, native herbaceous species: meadow goldenrod. These findings run counter to the general belief that herbivorous insects have only weak effects on terrestrial plant communities. Our results suggest that herbivores can typically regulate terrestrial plant communities. Numerous other studies also document the direct importance of herbivory in terrestrial plant communities (e.g., Spiller and Schoener 1990, Marquis and Whelan 1994, Chase 1998, Schmitz et al. 2000) and important interactions between herbivores and resource competition (e.g., Hunter and Price 1992, Ritchie et al. 1998, Chase et al. 2000), further strengthening this suggestion. Here, we not only show that insects can have important effects on terrestrial plant communities, but also identify when herbivorous insects should regulate plant communities. Herbivorous insects should regulate plant communities.
communities when they track host plant density, if their host plant is a competitively dominant species. In this study, damage to meadow goldenrod and the resulting increase in plant species richness occurred because of the ability of the specialist herbivore, Trirhabda virgata, to track goldenrod density.

Litter accumulation had the opposite effect of herbivorous insects on plant species richness. As predicted by the litter accumulation hypothesis, litter mass increased with the biomass of the dominant plant species, meadow goldenrod. This led to a decrease in species richness. Insects, however, alleviated the effect of litter by suppressing goldenrod biomass. Therefore, insects may have had a greater effect on the plant community than did litter, through their effects on the dominant plant species.

Acknowledgments

This work was supported by NSF grants BSR-8817961 and BSR-95 27536 to R. B. Root. W. P. Carson was supported by NSF grants DEB-95 27729 and DEB-95 15184 during manuscript preparation at the University of Pittsburgh. C. L. Mohler was supported, in part, by Hatch funds (Regional Project NE-92, NY(C) 183458) from the Cornell Agricultural Experiment Station. Peter Morin’s lab group provided valuable discussion on an earlier version of this work. We thank Jeremy Fox, Amy Long, Timon McPhearson, Peter Morin, Scott Meiners, Owen Petchey, Stefan Schnitzer, Henry Stevens, and Scott Wilson for comments on various drafts of the manuscript. We are particularly grateful to R. B. Root for numerous insightful discussions and comments. We owe a huge thanks to Greg Bartus, who assisted with the study during three key field seasons, and to Chris Asaro, Sean Boerke, Amatt Facenza, Amy Farstad, and Loden Mohler, who assisted with plant sampling in 1992.

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