HERBIVORY AND PLANT SPECIES COEXISTENCE: COMMUNITY REGULATION BY AN OUTBREAKING PHYTOPHAGOUS INSECT

WALTER P. CARSON1 AND RICHARD B. ROOT

Abstract. Most general theories proposed to explain the trophic structure of communities ignore the possibility that insect outbreaks can severely damage vegetation and reduce the abundance of dominant plant species over vast areas. Specialist chrysomelid beetles can irrupt and defoliate goldenrods (Solidago spp.), a group of widespread, long-lived, herbaceous perennials. We examined the long-term effects (10 yr) of suppressing insects, using insecticide in replicated plots on the structure and diversity of an old field dominated by the goldenrod, Solidago altissima. An outbreak of the chrysomelid beetle, Microrhopala vittata, that specializes on S. altissima, occurred during the experiment and persisted several years. Damage caused by this outbreak dramatically reduced the biomass, density, height, survivorship, and reproduction of S. altissima. Herbivore exclusion caused the formation of dense stands of goldenrods with a twofold increase in both standing crop biomass and litter. The understory in these dense stands had significantly lower plant abundance, species richness, flowering shoot production, and light levels; these conditions persisted for years following the outbreak. Thus, M. vittata functioned as a keystone species. Furthermore, insect herbivory indirectly increased the abundance of invading trees, thereby increasing the rate of succession, by speeding the transition of this old field to a tree-dominated stage.

We conducted two follow-up experiments to test the hypothesis that insects altered community dynamics by their indirect effect on litter accumulation and light availability in the understory. In the first experiment, we tied back the canopy to increase light into the understory and removed litter in both the insecticide-treated and control plots. We found little effect of removing litter. By contrast, increasing understory light levels significantly increased understory forb abundance and species richness. In the second experiment, we placed rosettes of Hieracium pratense, the dominant understory forb, under nine levels of shade cloth, ranging from 95% shade to full sun. Flowering-shoot production was a linear function of light availability ($r^2 = 0.92; P < 0.0001$). We concluded that insect herbivores indirectly promoted plant species richness and coexistence, primarily by augmenting light availability to suppressed understory species.

Insect herbivory may often play a strong role in goldenrod stands, because outbreaks will likely occur at least once, if not more, during the period when goldenrods are dominant. Furthermore, our findings provide compelling evidence for two general mechanisms whereby insect herbivory promotes plant species diversity and coexistence. The first mechanism operates during outbreaks when insects act as keystone species. The second mechanism can operate at less than outbreak levels and occurs whenever insect damage augments light to a sufficient degree to enhance the fecundity of suppressed nonhost species. If this increase in fecundity increases recruitment of subordinate species, then insect herbivory will promote plant species coexistence and diversity. Our data suggest that there is a continuum in the influence of insect herbivory on plant communities from the more subtle, but important, effects of herbivory on the fecundity of nonhost species to the devastating influence of outbreaks. Also, our results demonstrate that long-term experiments are required to elucidate the role of insect herbivores. Finally, we propose that insect outbreaks are common enough in many community types, particularly forests, to warrant explicit consideration in theories of trophic regulation, particularly in terrestrial communities inhabited by long-lived plant species.

Key words: chrysomelid; community regulation; competition and succession; goldenrods; herbivory; Hieracium pratense; litter; Microrhopala vittata; old field; phytophagous insects as keystone species; Solidago altissima; trophic regulation.

INTRODUCTION

Insect herbivores are rarely a major component of theories of community or ecosystem dynamics (Strong et al. 1995), although Wilson (1987) argued that invertebrates were more important in the maintenance of ecosystems than vertebrates. A number of theories of trophic-level interactions predict that herbivorous insects will have little influence on terrestrial vegetation, particularly on net primary production (e.g., Hairston et al. 1960, Slobodkin et al. 1967, Fretwell 1977, 1987, Oksanen et al. 1981, Oksanen 1988, 1990, Hairston

A different view holds that insects only damage or consume a small amount of their host plants, because most plant species are well defended or of low nutritional value (Murdoch 1966, Crawley 1989b; Hartley and Jones 1997). Lawton and McNeill (1979) suggested that herbivorous insects are caught between the interacting forces of predators and parasites on one hand and unpalatable or low quality plants on the other. Regardless of which view one holds, the outcome is the same: herbivorous insects will have a negligible influence on plant community structure, composition, and productivity (Edwards and Gillman 1987, Crawley 1989a, b, Pacala and Crawley 1992). Pacala and Crawley (1992) concluded that “herbivores often have little effect on communities,” although later Crawley (1997) concluded that there were an insufficient number of studies of insect herbivory from which to generalize.

The current debate regarding the regulation of communities and food webs has shifted from arguing whether regulation is top-down or bottom-up, to deciphering how these forces interact and when one force or the other has primacy (Fretwell 1977, Oksanen et al. 1981, Hunter and Price 1992, Power 1992a, Oksanen 1988, 1990, Leibold 1989, 1996). Insect herbivory, however, does not hold a prominent position in any of these theories (Hairston et al. 1960, Slobodkin et al. 1967, Oksanen 1990, Hairston and Hairston 1993). None seriously consider that some native insects are known to outbreak, and indeed many hold the view that these eruptions are “exceptions” (Hairston et al. 1960, and most recently Hartley and Jones 1997). It is during these eruptions, however, when insect herbivores may play a central role in community regulation and dynamics (Olff and Ritchie 1998). Just as the role of predators varies in space and time (Power 1992b, Chase 1998), it is likely that the role of insect herbivores will also vary in space and time (e.g., Huntly 1991, Bach 1994, Chase 1998, Olff and Ritchie 1998), due to characteristically large population fluctuations of some insect herbivores.

Overall, it is difficult to evaluate predictions generated by community-level theories because of the lack of relevant long-term community-level studies (Crawley 1989a, 1997, Huntly 1991). There is, however, ample evidence at the level of individuals and populations that phytophagous insects have strong effects on plant growth, fitness, distribution, recruitment, and interspecific competitive ability (reviewed by Hendrix 1988, Louda et al. 1990, Gange 1990, Marquis 1992, and Crawley 1997). Furthermore, data are slowly accumulating to demonstrate that native phytophagous insects can exert a strong influence on plant community dynamics among a number of community types, particularly during outbreaks (Morrow 1977, Morrow and LaMarche 1978, McBrien et al. 1983, Berdowski and Zeilinga 1987, MacLean 1988, Danell and Ericson 1990, Veblen et al. 1991, Fox and Morrow 1992, Bach 1994). Perhaps the most extensive work on the influence of insects on plant communities is that of Brown and Gange and colleagues, who studied early and mid-successional grasslands in England (Brown 1985, 1990, Brown et al. 1987a, 1988, Gibson et al. 1987, Brown and Gange 1989, 1990, 1992). They found that suppressing aboveground insects caused an increase in the abundance of the dominant perennial grasses and a decline in species richness. These studies, however, devoted little attention to the mechanisms underlying community change following herbivore exclusion. Many of the theories of trophic level interactions and trophic cascades require, or assume, knowledge of the mechanisms by which consumers alter population and community dynamics of lower trophic levels; yet this information for plants is scarce.

In this study, we examined the effects of suppressing insects with insecticides for 10 yr on the structure, composition, and diversity of an old-field plant community dominated by Solidago altissima. We asked whether the reduction of herbivorous insects would lead to the development of a different plant community, in terms of species fecundity, composition, standing biomass, and species richness. We also examined the underlying mechanisms responsible for any observed changes in the community by conducting experiments on the relationships among insect herbivory, litter accumulation, light availability, and plant species abundance and reproduction.

Materials and Methods

Study site and natural history

Study site.—We conducted this study in an old field at Whipple Farm, located several kilometers northeast of Ithaca, New York (42°25’ W, 76°31’ N). The climate is humid continental with a mean annual rainfall of ~960 mm. Most of this rainfall occurs during the growing season, which extends 146 d from early May to early October (Neeley 1961). The soil in this south-facing, gently sloping old field is a channery silt loam in the north (Typic Fragiochrepts) and a gravelly silt loam in the south (Typic Dystrochrepts; Neeley 1961). The old field (~150 × 60 m) was abandoned from agricultural practice at ≥10 yr prior to the start of the
experiment. Solidago altissima dominated the overstory; Solidago rugosa, Euthamia graminifolia, and Aster species were subdominant. Hieracium pratense and Fragaria virginiana were the two most abundant understory forbs, whereas Poa pratensis, Poa compressa, Agropyron repens, and Anthoxanthum odoratum were the most abundant graminoids. Other common forbs included Taraxacum officinale, Daucus carota, and Chrysanthemum leucanthumum. Two hedgerows ran along the long margin of the field and separated the site from two other large goldenrod-dominated old fields.


Experimental design

Design and insecticide application.—In 1982, Whipple field was divided into 112 5 × 4 m plots (8 × 14 array), each separated by 2-m mowed buffers. We randomly selected 30 of these plots and then randomly selected 15 of these to receive insecticide, and the remaining 15 served as untreated controls (see Plate 1). We applied insecticide at ~3-wk intervals, beginning in 1982 and continuing during the growing season for every year until 1992. We sprayed Fenvalerate (DuPont, Wilmington, Delaware, USA), a broad-spectrum synthetic pyrethroid that we have used successfully for
many years (Cain et al. 1991, Root 1996). Fenvalerate kills insects on contact, and, after application, residues remain on plants acting as antifeedants and oviposition repellents (Gist and Pless 1985). Fenvalerate was applied at a recommended rate of 300 g of active ingredient per hectare per application. Fenvalerate was mixed with water and applied early in the morning or late evening from early April through September using Solo backpack sprayers (Forestry Suppliers, Jackson, Mississippi). The amount of water used during insecticide application was negligible (3.8 L per 5 × 4 m plot), representing only a minute fraction of water received by rainfall.

**Insecticide selection.** — We are aware of potential pitfalls associated with insecticide experiments (Brown et al. 1987c, Crawley 1989b, Root 1996). Overall, Fenvalerate is an ideal choice for insect exclusion experiments. Fenvalerate has no phytotoxic effects on the plant species so far tested (Jones et al. 1986; E. I. du Pont de Nemours, unpublished reports), and plant toxicity trials conducted as part of this study revealed no phytotoxicity (see Materials and methods: Experimental design: Insecticide greenhouse trials). The foraging behavior of pollinators is little affected by Fenvalerate 24–48 h after application (Moffett et al. 1982, Mansour et al. 1984, David and Somasundaram 1985, Mayer et al. 1987). Furthermore, Fenvalerate is a long chain hydrocarbon containing only one atom of nitrogen (Thompson 1989), so repeated applications do not alter soil fertility (Root 1996). Talekar et al. (1983) found that Fenvalerate did not affect ammonification, nitrification, or soil microbial populations. Additionally, Fenvalerate will have minimal effects on belowground herbivory, because it has very low water solubility, tends to bind to surface soil and litter, and exhibits little leaching activity (Mikami et al. 1984). Fenvalerate has a short half-life and is broken down primarily by soil microbial activity (Miyamoto and Mikami 1983). Fenvalerate does not bioaccumulate in animals and plants (Onkawa et al. 1980, Bradbury and Coats 1982, Mumtaz and Menzer 1986, Lee et al. 1988). Fenvalerate is considered ideal for repeated use, because it is rapidly degraded and does not accumulate with repeated applications (Mikami et al. 1984, Talekar et al. 1983).

**Insecticide greenhouse trials.** — We conducted greenhouse trials to test whether Fenvalerate had a phytotoxic or growth-enhancing effect on five different common old-field species in the absence of insects. In early spring, we transplanted individual shoots and soil of each species from the field into pots in a greenhouse. Individuals were paired by size, and one of each pair (n = 8–15 pairs) was sprayed (SP) biweekly for one entire growing season with Fenvalerate at slightly higher concentrations and more frequently than field levels, while the other of the pair remained untreated (C). For several key species (e.g., *Solidago*), we measured total plant dried mass, inflorescence dried mass, and plant height. For some understory forbs, we tallied only the number of flowers produced, because flowering is a sensitive indicator of a phytotoxic or enhancing effect. Our data confirm previous published studies: application of Fenvalerate had no significant effect on individual plant weight or flowering shoot production. (Plant mass, in grams [mean ± 1 se]: *Daucus*, SP, 6.0 ± 0.83, C, 6.9 ± 1.2; *S. altissima*, SP, 10.2 ± 0.50, C, 9.2 ± 0.47; *S. rugosa*, SP, 66.7 ± 12.2, C, 64.3 ± 7.3. Peak number of flowering stems, in grams [mean ± 1 se]: *Chrysanthamum*, SP, 3.8 ± 1.5, C, 3.8 ± 1.2; *Daucus*, SP, 13.5 ± 2.3, C, 14.4 ± 0.9; *Hieracium*, SP, 18.2 ± 2.0, C, 15.8 ± 1.9. None of these comparisons were significant, based on paired t tests at P ≤ 0.05).

**Measurements of herbivore activity**

**Herbivore loads.** — We censused insect herbivores on the dominant species, *S. altissima*, in early June in every year during 1982–1991, except 1988. 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 usually higher than in the summer (Root 1996). Our sampling method is explained and justified in detail elsewhere (Root and Capuccino 1992, Root 1996), and here it 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 species that specializes on *S. altissima*) molted into the third instar. Throughout each plot, we selected 8–10 stems of *S. altissima* 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. The herbivore “load,” the dry mass of herbivores found on a given amount of plant material, was calculated by multiplying the abundance of each insect species by its mean mass and dividing by the total length of the stems examined in each plot (Root and Capuccino 1992, Root 1996).

**Plant damage.** — We quantified the percentage of leaf area damaged by leaf-chewing insects on the two most common canopy species (*S. altissima* and *S. rugosa*) and the two most common understory forbs (*Fragaria virginiana* and *Hieracium pratense*). Percentage damage was estimated by comparing damage on leaves to a template of artificial (paper) leaves, with 12 classes of damage: 0–1%, 1–5%, 5–10%, and in 10% increments up to 100% of area removed. We constructed the damage template by photocopying small and large leaves from real leaves of each species. We then punched holes in the paper leaves creating damage that approximated the midpoint of each of the damage classes. We used a LI-COR leaf area meter (LI-COR, Lincoln, Nebraska, USA) to determine the percentage of area removed with the hole punch on the paper leaves.

Leaves were collected in mid to late July for all four
species from each treatment in 1989, 1990, and 1991. For the Solidago species, we haphazardly selected (see Materials and methods: Measurements of herbivore activity: Herbivore loads for criteria) five to eight stems throughout each plot. We picked every third to fourth leaf moving down each stem, until between four and seven leaves were sampled. For Hieracium and Fragaria, we haphazardly harvested five to eight entire rosettes, with all attached leaves. Leaves of all species were placed in an envelope, frozen, and later analyzed. Mean leaf damage per plot for each species was calculated by multiplying the number of leaves within a given damage category by the midpoint of that category, adding the totals across all damage classes, and dividing by the number of leaves.

Environmental measurements

Soil fertility and soil moisture.—Soil fertility, including nitrate nitrogen, ammonium nitrogen, phosphorus, potassium, and magnesium, was analyzed in May 1990. Two 15-cm soil cores were collected from each of 10 plots from each treatment. Samples from each plot were pooled, air dried, and then analyzed by the Cornell University Nutrient Analysis Laboratory. Nutrients were extracted from the soil samples with Morgan’s solution (10% sodium acetate in 3% acetic acid, buffered to pH of 4.8) at a 5:1 solution to soil volumetric ratio. Nitrate nitrogen was determined using hydroxine reduction (American Public Health Association 1976), and ammonium nitrogen was determined using phenate–hypochlorate methods (Environmental Protection Agency 1979). Phosphorus was determined by the molybdenum blue method, using stannous chloride as a reducing agent. Total potassium was determined by atomic absorption spectrophotometry. We calculated percentage soil moisture gravimetrically for the top 10 cm of the soil for all treatments in mid-July of 1989 and mid-June of 1991. Two 15-cm soil cores were extracted from each plot, dried for 24 h at 105°C, and a pooled mean was determined for each plot.

Light penetration and leaf area index.—We measured photosynthetically active radiation (PAR), both above and below the canopy, using a LI-COR PAR point sensor on clear days between 1100 and 1200 on 8 September 1988, and at four times during the growing season in 1989: 22 May, 11 June, 30 June, and 25 August. The sensor was placed at 10 locations throughout each plot, ~20 cm above the litter layer. Finally, we used a LI-COR plant canopy analyzer to calculate the leaf area index (LAI) in early September 1991. We took four measurements in each corner of each plot in late evening, by placing the sensor ~20 cm above the litter layer. Measurement means were evaluated to obtain a single plot value.

Vegetation sampling

General approach.—We did not measure every response variable during the 10 yr of this study for several reasons. First, the labor required to sample every aspect of the vegetation would be too costly. Second, because some sampling procedures were destructive (e.g., biomass, individual plant harvests, rhizome production), frequent sampling could influence the results, particularly those pertaining to the slow-growing woody species. Consequently, we sampled a number of parameters in only a few years, typically near the end of the study. Additionally, based on our previous experience from studying the plant ecology of goldenrod-dominated old fields (Carson and Barrett 1988, Carson and Peterson 1990, Carson and Pickett 1990) and the ecology of goldenrod insects (Root and Cappuccino 1992, Meyer and Root 1993, Root 1996), we feel confident that we could detect any major shifts in herbivore activity or plant response by closely monitoring the plots. Therefore, we measured the density, height, and herbivore loads of S. altissima in nearly every year. When we began to observe the effects of insect exclusion on the abundance (density) of S. altissima, we expanded our sampling effort. This approach proved viable and efficient, although we acknowledge that we may have overlooked some of the subtle influences of insect herbivory earlier in the study.

Plant height and density.—We measured the height of the two most dominant canopy species (S. altissima during 1982–1991, and S. rugosa during 1988–1991) by measuring the height of 10–15 haphazardly selected stems scattered throughout each plot in September of each year (see Materials and methods: Measurements of herbivore activity: Herbivore loads for selection criteria). We tallied the density of Solidago altissima in three to five subplots during 1981–1990 that we randomly selected each year. Additionally, we determined the density of all canopy species in these subplots in 1988 and 1989. In mid-June, we quantified the densities of all understory forbs in each plot in 1988 and 1989, and also for the eight dominant understory forbs (Hieracium pratense, Fragaria virginiana, Taraxacum officinale, Daucus carota, Erigeron strigosus, Chrysanthemum leucanthemum, Potentilla simplex, and Carina vulgaris) during 1988–1990 and in 1992. We tallied the density in either two or four randomly selected 20 × 20 cm subplots. We calculated the density and stem basal diameter of woody species in two randomly (stratified) selected 2.6 × 1 m subplots in July 1991 in each plot.

Biomass.—We sampled the aboveground biomass of all plant species in two circular 1/8-m² quadrats, placed in a stratified random manner in all plots, in June and September of 1988 and 1989. We sampled biomass in only two years to avoid damaging the plots. Quadrats sampled in one year were not resampled. Because biomass of many understory species peaked in June, these data were used to compare the responses of understory species, whereas we used September samples to compare canopy biomass. All plants were dried at 80°C for
48 h and evaluated gravimetrically. We calculated species richness for each plot as the average of the number of species found in each of the two 1/8-m² quadrats at each sampling date. We also harvested seven or eight stems of *S. altissima* and *S. rugosa* in September during 1988–1992 and 1989–1991, respectively, to determine mean plant mass.

**Plant flowering.**—We counted the flowering stems throughout each 4 × 5 m plot, during the peak flowering periods for six of the most common understory forbs in three or four consecutive years (1988–1991), and for four common overstory species in 1990 and 1991. The understory species were *Hieracium pratense*, *Taraxacum officinale*, *Daucus carota*, *Erigeron strigosus*, *Chrysanthemum leucanthum*, and *Carlina vulgaris*, and the overstory species were *Solidago gigantea*, *S. juncea*, *Aster sagittifolius*, and *A. novae-angliae*. We chose these species because they were common and their inflorescences or flowering shoots could be easily seen and quantified. Unlike the other forbs, we determined the density of *H. pratense* in two randomly selected 1-m² subplots, because this species was so abundant. We could not reliably count the flowering stems of *S. altissima* and *S. rugosa*, because they were too abundant. Instead, we determined mean inflorescence mass of these species using the stems harvested for plant biomass. Finally, we calculated the proportion of the stems that bloomed for 20 randomly selected individuals of *S. altissima* and *S. rugosa* in 1991.

**Goldenrod demography.**—We marked all stems of *S. altissima* in 1989 and 1990, in two permanent 60 × 60 cm subplots, located in a stratified random manner in each plot. Stems (~1000 stems/year) were censused as they emerged in early May and again in mid-July and mid-September, when we recorded final stem heights. Additionally, in May of 1991, we counted the number of mature rhizomes that were produced by three to five randomly selected aboveground stems of *S. altissima* that had senesced the previous fall in the two permanent 60 × 60 cm subplots (Cain et al. 1991). We considered a rhizome mature, if it had emerged from the old parent ramet and had an active apical meristem. We limited our sampling of rhizomes to only one year to minimize localized soil disturbance caused by clone excavation.

**Litter accumulation and decomposition.**—We measured litter depth in each corner of two randomly selected 1-m² subplots on 2 May 1989. Litter mass was sampled in June in 1988 and 1989, by collecting all of the litter in the 1/8-m² quadrats used to measure live biomass. We also collected plant litter as part of a separate experiment in two larger subplots (100 × 50 cm), placed in a stratified random manner within each plot in June of 1990. Litter was dried at 80°C and evaluated gravimetrically. We compared rates of litter decomposition in 1991 by placing 5 g of dried litter into 10 × 20 cm mesh nylon bags (mesh size = 3 mm). The litter originated from each insecticide-treated and control plot, and it was placed back into its plot of origin. We placed eight bags within the litter layer in mid-May in each treatment, so that each bag was flush with the natural litter surface. Four randomly selected bags were collected on 17 July, and the remaining four were collected on 25 September. We dried the bags and measured percentage mass loss.

**Mechanistic experiments**

The long-term exclusion of insects led to major changes in this old-field community. We conducted two follow-up experiments to ascertain the mechanism by which herbivores altered plant reproduction, density, biomass, and species richness.

**The influence of shade on flowering in *Hieracium pratense***.—We tested the hypothesis that low light controlled flower production in *Hieracium pratense* (the most common understory forb). To test this hypothesis, we built shade houses using nine different levels of spectrum-neutral shade cloth: full sun, 30%, 47%, 55%, 63%, 73%, 80%, 85%, and 95% shade). Spectrum-neutral shade cloth (Hummert Greenhouse Supply, Earth City, Missouri, USA) alters light quantity, but not light quality (e.g., red:far red ratios). Each shade house was 100 cm long × 60 cm wide × 60 cm high, and was enclosed on the top and three sides by the specified shade level. We left the north side of each house open to allow access and airflow. The shade houses were placed on a mowed grassy field at the Cornell Experimental Ponds facility, in a 9 × 5 array of randomized design, with each shade level replicated five times. We transplanted *Hieracium* rosettes from an old field adjacent to the Whipple site into pots filled with a 1:1 peat:soil mixture, and fertilized with slow-release fertilizer. Fifteen pots, each with a single *Hieracium* rosette, were placed under each shade house, between 24 April and 4 May 1991, and watered regularly. We measured light availability at five locations under each shade house near midday on a clear day with a LI-COR PAR point sensor; analyses were conducted using the mean light availability. We recorded the total number of flowering stems produced by each ramet during flowering, as well as the number of new ramets produced by rhizomes at the end of the growing season.

**The influence of enhancing light and removing litter on understory plants.**—We tested the hypothesis that shade and litter accumulation altered the density, cover, species richness and flowering of understory species. We altered understory light availability and litter quantity in two randomly selected 1-m² subplots in 13 of the 15 spray and control plots. In one of the 1-m² subplots, we reduced the shade produced by the canopy by pulling back tall species (>40 cm) beyond the perimeter of each plot and tethering them with nylon twine attached to corner stakes. The canopy of the other 1-m² subplot was left unmanipulated. This treatment
did not appear to injure manipulated plants and left plant roots intact (Carson and Pickett 1990). Tall plants were tied back beginning in mid-May and subsequently when necessary during the growing season from 1990–1992. Additionally, litter that had accumulated in a randomly selected half of each of the 1-m² subplots was carefully removed in late April or early May of each year by hand, so as not to disturb the soil surface. Additionally, we did not remove the thin layer of litter in contact with the soil surface to avoid disturbing the soil.

Immediately after these manipulations, we placed four permanent 20 × 20 cm quadrats (in a 2 × 2 array), in each of the two 1-m² subplots; two quadrats were placed on the side with litter, and two were placed on the side where litter had been removed. We determined the presence and absence of all species and determined the density of the seven most abundant understory forbs within each quadrant during 6–15 June 1990. These species were Hieracium pratense, Fragaria virginiana, Taraxacum officinale, Daucus carota, Chrysanthemum leucanthum, Potentilla simplex, and Carlina vulgaris. We also visually estimated the total plant cover of the entire understory. Additionally, we counted the total number of flowering stalks of Hieracium pratense in each 1-m² subplot, but we did not specify whether these stalks were initially on the side that had the litter removed or on the side where the litter was left intact. Consequently, we were not able to test the role that litter plays in flower production of H. pratense. We recensused these quadrats during 26 June–10 July 1992. Data are reported as percentage change in total species density, total understory cover, and species richness, and the change in the number of flowering stalks of H. pratense.

**Statistical analysis**

To test for effects of long-term insect suppression (i.e., insecticide treatment), we used repeated measures ANOVA analyses (PROC MIXED in SAS/STAT version 6.12; SAS 1997). All model statements were written following Little et al. (1996:97). In all repeated measures analyses, we used the first-order autoregressive covariance structure (REPEATED/TYIE = AR(1)). This option assumes that samples are correlated through time, and the degree of correlation decreases with time (Little et al. 1996). For the tie-back and litter-removal experiment, we tested the combined effects of herbivore reduction, light, and litter on percentage change of the following quantities: total density, total cover, species richness, and flower production of Hieracium pratense. To test these effects, we used a split-split plot design, with three treatment factors (modified from Lenter and Bishop 1986:373). In these experiments, we randomly assigned insecticide treatment to whole plots, so pesticide was completely randomized. We then nested both light treatments (tie-backs and controls) within each plot type (sprayed or unsprayed), and nested both litter treatments (litter removal and controls) within each light treatment. Thus, the spray was completely randomized with respect to whole plots, but light was nested within whole plots, and litter was nested within each light treatment (Neter et al. 1996). We used PROC MIXED for this analysis (Little et al. 1996). We additionally used the default covariance structure, which provides a separate variance estimate for each random effect (SAS 1997). We used Statview for the regressions and t tests. Rather than include numerous tables, we placed the P values of all the tests in their respective figures. All data were transformed as necessary to reduce heteroscedasticity.

**Results**

**Insect herbivore loads and plant damage**

Insect herbivore loads on Solidago altissima were low at the beginning and end of the study, but were at outbreak levels in 1986 and 1987 (Fig. 1). More than 95% of the herbivore load in 1986–1987 was accounted for by Microrhophula vittata (Root 1996), one of two chrysomelid beetles that periodically outbreak and reach very high population densities on S. altissima (Cappuccino 1991, Root and Cappuccino 1992). These leaf-mining beetles are commonly found in the majority of Solidago-dominated old fields in this region (Root and Cappuccino 1992) and do the bulk of their damage as larvae, the stage at which they were censused in this study.

Insecticide application significantly reduced the mean area damaged by insects on leaves of S. altissima, S. rugosa, and Fragaria virginiana in each of three consecutive years (Fig. 2). Insecticide treatment did not reduce damage on Hieracium pratense in any year (Fig. 2), although mean area damaged was always <3%. Damage varied significantly (P ≤ 0.05) among years for all the species, except for S. altissima. Damage levels were determined after the outbreak of M. vittata ended and, thus, represent levels of damage experienced by S. altissima in nonoutbreak years. During the outbreak, individuals of S. altissima suffered heavy damage. Our estimates of total insect damage are probably conservative, because some herbivores damage plants in cryptic ways: (1) by xylem or phloem tapping, and (2) by causing the more rapid loss of damaged leaves (Crawley 1997). Our data on both insect herbivore loads on S. altissima (Fig. 1) and measures of plant damage (Fig. 2) show that insecticide application effectively reduced both insect numbers and insect damage. Similar experiments in nearby younger old fields (1–3 yr) demonstrated that insecticide application reduced damage on many other species including graminoids (Carson and Root, in press).

**Environmental measurements**

**Light.—**The percentage of ambient light reaching the understory was four times greater in control (C) plots
FIG. 1. Comparison of mean (± 1 SE) herbivore loads, mean stem height, and mean stem density of *S. altissima*, as well as mean stem height only for *S. rugosa*, in insecticide-treated (sprayed) and control plots. Insecticide was applied at 3-wk intervals during each growing season. Some error bars are too small to be visible. *P* values reported in the top left corner of each graph represent repeated-measures ANOVA and test whether there was a significant effect of the spray treatment *(S)*, a significant effect of year *(Y)*, and a significant spray × year interaction *(S × Y)*.

than in sprayed (SP) plots in September of 1988 (mean ± 1 SE: SP, 11 ± 1.4%; C, 43 ± 4.1%) (*t* test, df = 28, *P* < 0.0001). Light availability in the understory dropped sharply from 22 May to 11 June 1989, but this decline was much greater in the sprayed plots (Fig. 3). Understory light levels remained higher in the controls throughout the growing season. The leaf area index (LAI) was significantly higher in sprayed plots near the end of the growing season on 4 September 1991 (mean ± 1 SE: SP, 3.0 ± 0.13; C, 2.0 ± 0.12) (*t* test, df = 28, *P* < 0.0001). These results demonstrate that for three consecutive years (1989–1991) light was much lower in the understory of the insecticide-treated plots.

**Population and community responses to long-term insect exclusion**

**Height.**—Insect suppression led to an increase in the height of *S. altissima* in the fourth year of insecticide application (1984; Fig. 1) and for seven years thereafter. Insect suppression also significantly increased the height of *S. rugosa* during 1988–1991, the only years we measured this species (Fig. 1).

**Plant density: canopy species.**—Although insect suppression increased the height of *S. altissima* by the fourth year, it did not alter stem densities until 1988, the eighth year of the study (Fig. 1). In 1986 and 1987, an outbreak of *Microrhopala* (Fig. 1; also see Root [1996]) severely defoliated stems throughout the control plots and caused a crash in goldenrod density in 1988. This crash in stem density was likely brought about directly by stem death, and indirectly by a decline in new rhizomes produced by weakened stems that survived the outbreak (Table 1; Cain et al. 1991). Overall, this outbreak further reduced goldenrod height (Fig. 1) and thinned the canopy, thereby creating gaps that were not filled completely by other canopy species. Specifically, we did not find a significantly higher density of the next most abundant canopy species, *S. rugosa*, nor
February 2000

INSECT HERBIVORY AND COMMUNITY REGULATION

FIG. 2. Comparison of the percentage of leaf area damaged by leaf-chewing insects on the two most common goldenrods and the two most common understory forbs. Some error bars are too small to be visible. Damage estimates were determined two years after an outbreak of *Microrhopala*; they represent more typical levels of insect damage on *S. altissima* during the study. Values reported at the top of each graph are *P* values from repeated-measures ANOVA for the effects of spray treatment (S), year (Y), and their interaction (S × Y).

FIG. 3. Percentage of ambient photosynthetically active radiation (PAR) reaching the understory during the growing season of 1989, in sprayed and control plots. Some error bars are too small to be visible. *P* values reported on the graph represent repeated-measures ANOVA and test whether there was a significant effect of the spray treatment (S), a significant effect of date (D), and a significant spray × date interaction (S × D).

Plant density: understory forbs and woody species.—Control plots had a significantly higher density of most of the common understory forbs during 1988–1992 (Fig. 5). The only clear exception was *Fragaria virginiana*, which was not significantly different between treatments (Fig. 5). When we counted all forbs, control plots had nearly double (1988), or more than double (1989), the density compared to sprayed plots (Fig. 5). The large increase in the density of all forbs in control plots from 1988 to 1989 suggests that these species increased in abundance because of the insect outbreak the previous year that created a newly opened canopy (note the significant spray × year interaction). The control plots had more than double the density of the woody species *Viburnum dentatum, Fraxinus amer-*
TABLE 1. Comparison of mean (± 1 SE) percentage stem mortality and the mean number of mature rhizomes produced per stem of *Solidago altissima* in sprayed and control plots.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Treatment</th>
<th></th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem mortality (%) 1989</td>
<td>Spray</td>
<td>14.10 ± 1.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Control</td>
<td>23.50 ± 3.3</td>
<td>†</td>
</tr>
<tr>
<td>Stem mortality (%) 1990</td>
<td>Spray</td>
<td>9.80 ± 1.4</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Control</td>
<td>7.30 ± 1.5</td>
<td>†</td>
</tr>
<tr>
<td>No. rhizomes produced per stem 1990</td>
<td>Spray</td>
<td>1.35 ± 0.08</td>
<td>0.032‡</td>
</tr>
<tr>
<td></td>
<td>Control</td>
<td>1.08 ± 0.08</td>
<td></td>
</tr>
</tbody>
</table>

*Note:* There was much higher stem mortality in the control plots, relative to sprayed plots in 1989, but little difference between treatments in 1990.

† *P* values for stem mortality were as follows: *S*, 0.5511; *Y*, 0.0001; *S × Y*, 0.0096. These values represent repeated-measures ANOVA, and they test whether there was a significant effect of the spray treatment (*S*), a significant effect of year (*Y*), and a significant spray × year interaction (*S × Y*).

‡ Data for rhizome production were compared with a *t* test.

icana, and for all woody species combined (Fig. 6). Insecticide treatment did not influence the mean basal area of woody species (mean ± 1 SE: **S**, 0.57 ± 0.05 cm; **C**, 0.66 ± 0.04 cm) (*t* test, *df* = 28, *P* = 0.142).

**Canopy biomass.**—Insect herbivory dramatically reduced the total biomass, total canopy biomass, and the biomass of *S. altissima* in 1988 and 1989 (Fig. 7). The greater canopy biomass was accounted for entirely by *S. altissima*. When this species was excluded from the analysis, total canopy biomass was significantly higher in control plots (Fig. 7); this occurred because of small but consistent increases in the biomass of other canopy species (Fig. 7) that paralleled increases in the density of these species (Fig. 4). Insect herbivory sharply reduced the mean plant mass of *S. altissima* from 1988 to 1992, but did not influence *S. rugosa* during 1989–1991 (Fig. 8).

**Understory biomass.**—Total understory biomass was
Fig. 5. Comparison of mean (± 1 se) densities of all understory forbs combined (1988–1989 only) and common understory forbs, during 1988–1992, in sprayed and control plots. *H. pratense* and *F. virginiana* were the two dominant understory forbs. Densities were not determined in 1991. Note that the axis in the right column of graphs differs from the other two columns. Some error bars are too small to be visible. *P* values reported on each graph are from repeated-measures ANOVA for the effects of spray treatment (S), year (Y), and their interaction (S × Y).

Reduced by >50% in sprayed plots (Fig. 9). Forbs accounted almost entirely for this difference, because we could not detect any significant effect of spraying on the biomass of graminoids (Figs. 9). Overall, the biomass of the most common understory forbs, particularly *H. pratense*, was nearly always lower in sprayed plots (Fig. 9).

**Species richness.**—Species richness was significantly higher in the control plots, in both the spring and fall of 1988 and 1989, for both canopy and understory species, although the largest differences occurred in the understory (Fig. 10). We also determined mean species richness in 1990 and 1992 using the data from the smaller plant density subplots (20 × 20 cm), which we sampled as part of the canopy tie-back and litter-removal experiment. We only used subplots that were unmanipulated (i.e., intact canopy and litter), which allowed us to determine whether species richness still differed between treatments later in the experiment. Total species richness was significantly higher in control plots in both 1990 (mean ± 1 se: SP, 7.0 ± 0.54; C, 10.5 ± 0.57) (*t* test, *P* = 0.0002) and 1992 (mean ± se: SP, 7.0 ± 0.78; C, 11.7 ± 0.77) (*t* test, *P* = 0.0003).

**Flowering.**—Control plots had a much greater density of flowering shoots of six of the most common understory forbs through four consecutive years (1988–1991; Fig. 11). The effect was greatest for *H. pratense*, which had >10× as many flowering stalks per square meter than sprayed plots in 1989. Tremendous variation in flowering across years led to highly significant year effects for all understory species. For example, there
were numerous flowering stems of *D. carota* in control plots in 1988 and 1989, but almost none thereafter. Additionally, as shown in Fig. 12, we found a highly significant positive linear relationship between light availability in the understory and both the flowering of *Hieracium pratense* (*n* = 30; *r*² = 0.42, *P* < 0.0001) and the flowering of a group of understory forbs (*n* = 15, *r*² = 0.44, *P* < 0.0001). We also found a highly significant negative relationship between the log of the biomass of *S. altissima* and both the flowering of *Hieracium pratense* (*n* = 30; *r*² = 0.54, *P* < 0.0001) and the flowering of this same group of understory forbs (second order polynomial, *n* = 15, *R*² = 0.74, *P* < 0.0001).

The influence of herbivory on the density of flowering shoots in canopy species varied widely (Fig. 11). For instance, *S. juncea* had a higher number of flowering stems in sprayed plots in 1990, but not in 1991. In contrast, *A. sagittifolius* had a high number of flowering stems in control plots in both years, whereas the other two canopy species, *S. gigantea* and *A. nova-angliae*, showed no significant response. For the two most abundant *Solidago* species, we measured mean flower mass per stem. Insect herbivory caused a large decrease in inflorescence mass and proportion of stems of *S. altissima* that bloomed; herbivory, however, had no effect on *S. rugosa* (Figs. 8 and 13; also see Root [1996]).

**Demography.**—Insect suppression significantly reduced the mortality of *S. altissima* ramets in 1989, but not in 1990, and significantly increased the number of rhizomes produced per ramet in the spring of 1991 (Table 1).

**Litter accumulation and decomposition.**—Litter mass was significantly higher in sprayed plots during 1988–1990 (Fig. 14), and more than twice as deep in sprayed plots in May of 1989 (mean ± 1 SE: SP. 7.8 ± 0.60 cm; C. 3.2 ± 0.55 cm) (*t* test, df = 28, *P* < 0.0001). Litter decomposition was significantly higher in sprayed plots during the 1991 growing season (Fig. 14).

**Mechanistic experiments**

*The influence of shade on flower production in Hieracium pratense.*—The mean number of flowering stems produced per rosette in *H. pratense* increased linearly with light availability (*r*² = 0.92, *P* < 0.0001; Fig. 15). Rhizome production showed a different response (second order polynomial, *R*² = 0.68, *P* < 0.0001; Fig. 15). At very low light levels, (5% of ambient), rhizome production was low, but increased rapidly at slightly higher light levels (15% of ambient); it continued to increase, until leveling off at ~75% of ambient light.

*The influence of enhancing light and removing litter on the understory.*—We tested the hypothesis that low light and dense litter caused the poor performance of understory species found in the sprayed plots. In this experiment, any increase in cover or density during the two years of the experiment depended on the initial plant cover, density, and species richness at the beginning of the experiment. Therefore, all data are reported as the percentage change for each response variable (1990–1992).

Both increasing understory light by tying back the canopy and removing litter led to a significant increase in species richness (Fig. 16; *P* < 0.0001 and *P* = 0.001, respectively). Because there was both a significant spray × tie-back interaction (*P* = 0.053) and a significant spray × litter interaction (*P* = 0.019), these responses depended upon whether manipulations were conducted in spray or control plots. Specifically, as predicted, removing litter and tying back the canopy led to a larger increase in species richness, when nested inside sprayed plots where understory light levels were much lower and understory litter levels much higher (Figs. 3 and 14).

Tying back the canopy caused a substantial increase in understory cover (*P* = 0.002), but this increase occurred only in the insecticide-treated plots where a thick canopy was present (Fig. 16; spray × tie-back interaction, *P* = 0.008). Tying back the canopy also led to a significant increase in the combined density of the seven most abundant understory forbs (Fig. 16; *P* = 0.004; *Hieracium pratense*, *Fragaria virginiana*, *Taraxacum officinale*, *Daucus carota*, *Chrysanthemum leucanthemum*, *Potentilla simplex*, and *Carlina vulgaris*). Although this increase was much greater within the sprayed plots, there was only weak evidence for a spray × tie-back interaction (*P* = 0.097). This suggests that light was limiting to understory species, even in the control plots, over the duration of the experiment. Surprisingly, there was never a significant effect of removing litter on either density or cover, which sug-
suggests that light was the primary factor limiting plant abundance. Low initial abundance and high plot-to-plot variability of individual species precluded individual species-level comparisons.

*H. pratense* was the only species sufficiently abundant to test for effects of tying back the canopy on increased flowering-shoot production. Increasing understory light led to an increase in flowering in both the insecticide-treated and control plots (Fig. 16; $P = 0.001$). There was no significant spray × tie-back interaction ($P = 0.721$), which suggests that the canopy, even in the control plots, was preempting light (see Fig. 3) and reducing flower production in the understory. These results are consistent with those from the shade cloth experiment, where ramets of *Hieracium* in full sun produced more flowering shoots than ramets receiving 70% of full sun.

**DISCUSSION**

*Response of the overstory to insect herbivory*

Long-term insect suppression led to the development and maintenance of a robust stand of *S. altissima*, with nearly three times the canopy biomass and twice the total biomass of unsprayed plots (Figs. 1, 7, and 8). The biomass of *S. altissima* accounted for the entire difference in biomass between treatments (Fig. 7). Insect herbivory initially reduced only the height (Fig. 1) and mass of individual stems (Root 1996), but following an outbreak of the chrysomelid beetle *Microphala vittata* in 1986 and 1987, herbivory caused a crash in stem density in 1988 (Fig. 1). By 1989, insect herbivory had reduced the height and density of *S. altissima* by nearly 50%. In insecticide-treated plots, we regularly encountered robust individuals $>150$ cm...
tall, and occasionally >200 cm tall. Throughout much of the northeastern and midwestern United States, *Solidago altissima* (or *S. canadensis*) is the dominant herbaceous canopy species in early and midsuccessional old fields (Mellinger and McNaughton 1975, Werner et al. 1980, Carson and Barrett 1988, Carson and Pickett 1990, Vankat and Snyder 1991, Bazzaz 1996). Goldenrods are often nitrogen limited in old fields (Mellinger and McNaughton 1975, Carson and Barrett 1988, Carson and Pickett 1990), and here we demonstrate that insect herbivory can also dramatically limit goldenrod abundance over many years.

The other canopy species, all of which are clonal, did not spread to fill gaps in the canopy left by the demise of *S. altissima* (Fig. 4). The increase in the abundance of *Euthamia graminifolia* in control plots (Figs. 4 and 7), did not nearly compensate for the decline in *S. altissima*. Furthermore, there was no difference between treatments in the abundance of the second most common canopy species, *S. rugosa* (Figs. 4 and 7). *S. rugosa*, however, could only spread in the sprayed plots, where a robust stand of *S. altissima* stood in the way. Consequently, any potential release of *S. rugosa* from herbivory in sprayed plots may have been stopped by the effects of interspecific competition with *S. altissima* (e.g., Armesto and Pickett 1985). Indeed, there is evidence that herbivory reduced the vigor of *S. rugosa*; stems were significantly taller in sprayed plots for four consecutive years (Fig. 1). Additionally, herbivory caused significant leaf damage on *S. rugosa* in three consecutive years (Fig. 2), and insect herbivory decreased the abundance of this species in a nearby younger old field (Carson and Root, in press). Furthermore, we found a highly significant positive correlation between damage on *S. altissima* and *S. rugosa* in control plots in two of three years (1989, \( n = 15, r^2 = 0.73, P < 0.0001 \); 1991, \( n = 15, r^2 = 0.71, P < 0.0001 \)). This correlation is not surprising, because many of the specialist insects of *Solidago altissima* will also feed on *S. rugosa* (Messina and Root 1980, Root and Cappucino 1992). Consequently, insect herbivory may have prevented, or more likely delayed, *S. rugosa* from filling gaps in the canopy. Other canopy species (e.g., *E. graminifolia* and *Asters* spp.) did not fill in the overstory, probably because they were initially not very abundant, or because they produce a relatively small number of short rhizomes (e.g., *E. graminifolia*; Werner 1976), which may limit their rate of clonal expansion into gaps. Whatever the reasons, herbivory caused the long-term thinning of the overstory.
Response of the understory to insect herbivory

Abundance and species richness.—Insect herbivory, and in particular the damage caused by an insect outbreak, indirectly led to a long-term increase (≥5 yr) in the abundance of understory forbs and woody species, as well as an increase in species richness (Figs. 5, 6, 9, and 10). Several lines of evidence strongly suggest that herbivory caused these changes primarily by increasing light availability to understory species. Sprayed plots had much lower light reaching the understory throughout the growing season (Fig. 3) and a much higher LAI. Moreover, increasing understory light levels by tying back the canopy increased understory density, cover, and species richness in sprayed plots (Figs. 16). In contrast, these same manipulations had little influence on control plots (Figs. 16), where prior herbivory had created a more open canopy. There was little evidence that a reduction in soil resources caused the decline in understory species in the sprayed plots, though soil resources were only measured once. Consequently, herbivory may have indirectly caused an increase in soil resources, particularly during the outbreak, that may have played a partial role in increasing understory diversity and abundance. For example, Brown (1994) found that *Trirhabda* beetles feeding on goldenrods indirectly increased soil nitrogen and moisture levels as well as understory light levels. Additionally, Carson and Pickett (1990) found that species richness in goldenrod communities was controlled by an interaction between water and light availability. Although these other resources were likely involved, our experiments demonstrate a very strong indirect effect of herbivores on augmenting light availability to understory species.

Litter removals through three consecutive growing seasons did not lead to a significant increase in understory cover or density, even when the canopy was tied back to increase understory light levels (Figs. 16). Removing litter, however, did lead to an increase in species richness, and, as predicted, this increase was much greater in sprayed plots where the litter mat was twice as thick. Apparently, the thickness of the litter mat that accumulated in the sprayed plots was insufficient to reduce plant abundance, but did cause a reduction in species richness (see also Carson and Peterson [1990]).
Fig. 10. Comparison of mean (± 1 se) species richness in the canopy and understory in the spring and fall of 1988 and 1989, in sprayed and control plots. Some error bars are too small to be visible. Control plots also had significantly higher species richness in 1990 and 1992, as determined from smaller 20 × 20 cm density subplots (see Results: species richness). P values reported on each graph are from repeated-measures ANOVA for the effects of spray treatment (S), season (M), their interaction (S × M), and the three-way interaction with year (S × M × Y).

Palatability and the response of understory species.—Insect herbivory is most likely to benefit unpalatable understory species, but unlikely to benefit more palatable ones. For example, Hieracium pratense was, by far, the most dominant understory species in control plots (Figs. 5 and 9), and trichomes coating its leaves protect it from insects (Schmitz 1994). Correspondingly, we found low levels of leaf damage on this forb (Fig. 2). Furthermore, this species is introduced (Gleason and Cronquist 1991), and may suffer little damage, because it has potentially left behind its native herbivore fauna. Conversely, Fragaria virginiana is native and very palatable (Schmitz 1994), and we found significant insect damage on this species in three consecutive years (Fig. 2). Fragaria was the only common understory forb that was not more abundant in control plots (Figs. 5 and 9) where the canopy was more open, suggesting that insect herbivory may have restricted the spread of this species. Fragaria may not have spread in sprayed plots following release from herbivory, due to shading by the canopy (Carson and Pickett 1990). Overall, these findings are consistent with part of Leibold’s (1989, 1996) edibility hypothesis, which predicts that resistant plants will increase in abundance, if herbivore biomass increases and productivity is held constant (see also Schmitz [1994]). These findings also fit the concept of “escape competition” (Menge and Sutherland 1987); competition among well-defended prey (Hieracium in control plots at high abundance) occurs only after consumers (Microrhaphala beetles) have sharply reduced superior competitors (goldenrods).

Flowering and rhizome production.—A dense goldenrod canopy dramatically reduced the number of flowering shoots of understory forbs in insecticide-treated plots (Fig. 11). This reduction was probably caused, in part, by an increased failure of rosettes to produce flowers, not only to a decline in the density of rosettes. For example, in 1989, there were 42%, 63%, and 75% declines in densities of Taraxacum, Chrysanthemum, and Hieracium, respectively, in sprayed plots (Fig. 5), but there were 88%, 87%, and 92% respective declines in the production of flowering stems in sprayed plots (Fig. 11). Moreover, the frequency of Hieracium rosettes that produced flowers was 20% in control plots, but only 4% in sprayed plots in 1989 (from 20 randomly selected individuals per plot, n = 15, P < 0.0001; Mann-Whitney U test). We found that a decrease in light caused a linear decrease in flower production in Hieracium (Fig. 15). Hieracium usually flowers in early June, when understory light levels in the sprayed plots are already low enough (~20% of ambient; Fig. 3) to reduce the percentage of rosettes that flower (Fig. 15). Flower production was far more sensitive to shade than rhizome production (Fig. 15). Therefore, even beneath dense canopies, some individuals of Hieracium were probably producing new rosettes from rhizomes. This may explain why we observed a 91% decline in flowering shoots, but only a 75% decline in ramet densities in sprayed plots.

The overall response to herbivory

We provide the following scenario to describe the influence of foliar insect herbivory on this old-field community. Insect herbivory, particularly following an outbreak, defoliates the stems of the dominant canopy species. This, in turn, increases stem mortality and reduces new rhizome production, thereby reducing canopy biomass and density. A reduction in canopy biomass and density creates a sparse overstory that cannot be quickly filled in by other overstory species, because they spread slowly through clonal growth and are also
FIG. 11. Comparison of mean (±1 SE) number of flowering stems of common understory and overstory forbs during peak flowering, in sprayed and control plots. Some error bars are too small to be visible. Note that the axes vary for several of the graphs. Also note that values represent the number of flowering stems per 20 m², except for \( H. \text{ pratense} \), where the values represent the number of flowering stems per square meter. \( P \) values reported on each graph are from repeated-measures ANOVA for the effects of spray treatment \((S)\), year \((Y)\), and their interaction \((S \times Y)\).

In our study, the common forbs are native, whereas the common grasses are introduced (Gleason and Cronquist 1991); in England, the situation is reversed (Brown et al. 1987b). Because insect pressure is likely to be higher on the native herbs in their respective communities (Brown et al. 1987b), these findings are not necessarily at odds (cf. Hendrix et al. 1988, Brown 1990) and suggest that insect herbivores may typically have a strong influence on the dominant native herbaceous vegetation.

Our findings build upon previous studies in several ways. First, we tracked an outbreak of a specialist chrysomelid beetle that functioned as a keystone species (sensu Paine 1966; see also Strong [1992] and Menge et al. [1994]), which, by reducing the abundance of the superior competitor, increased the abundance and diversity of subordinate species for many years. These findings provide one of the first clear demonstrations of keystone species operating in a terrestrial community (Strong 1992). Second, our experiments identified a major mechanism by which phytophagous insects can mediate these changes in plant communities. Specifically, herbivores are capable of thinning canopies, thereby increasing light levels to a sufficient degree to release understory species. Third, insect herbivory, in-
directly through its effects on the canopy, can increase flowering-shoot production and, thereby, fecundity of understory forbs (see also Danell and Ericson [1990]). Finally, we found that insect herbivory on goldenrods indirectly increased the abundance of early successional trees and shrubs, thereby speeding the transition of this old field to a shrub- and tree-dominated stage. This runs contrary to generalizations that foliar insect herbivory retards or delays succession during early and midsuccessional stages (Brown 1990, Brown and Gange 1992, Davidson 1993). Previous studies were not of a sufficient duration to evaluate the responses of longer lived woody species.

Do insect herbivores typically regulate old-field communities?

The generality of our results depends upon the frequency of significant insect herbivory over the period when goldenrods dominate. Solidago altissima and S. canadensis are dominant very early in succession, and they can persist as dominant or abundant species for 20 yr, or for much longer (Bard 1952, Quarterman...
1957, Bazzaz 1968, 1996, Mellinger and McNaughton 1975, Werner et al. 1980, Armesto and Pickett 1985, Carson and Barrett 1988, Maddox et al. 1989, Vankat and Snyder 1991). Root (1996; see also Root and Cappuccino 1992) concluded, through long-term experiments and extensive surveys in central New York, that a population outbreak of one of the herbivores of *S. altissima* would occur on the order of once “every 5–15 yr.” Consequently, a given stand of goldenrod in the region of the study may, on mean, experience an outbreak anywhere from one to four times. In the region of our study, two genera of chrysomelid beetles are codominant and often outbreak, specifically *Microrhopala* and *Triirhabda* (Root and Cappuccino 1992). The impact of these chrysomelid beetles on goldenrods appears to be important in other regions as well. For example, Reid and Harmson (1974) noted that *Triirhabda* was a major pest of goldenrods in Ontario, Canada, and McBrien et al. (1983) followed an outbreak of *Triirhabda* in Ontario that devastated a population of *S. canadensis*. Werner et al. (1980) also noted the devastating effects of *Triirhabda* beetles on *Solidago canadensis* in Michigan, USA, and Carson (personal observation) found that outbreaks of these beetles could completely defoliate patches of *S. gigantea* in central Minnesota, USA (see also Brown 1994).

There is strong evidence that *Triirhabda* beetles emigrate from heavily infested or defoliated goldenrod patches, and they preferentially colonize and aggregate in robust or lush patches. Herzig (1995) and Herzig and Root (1996) demonstrated experimentally that dense aggregations of beetles will trigger beetle emigration in both sexes. By then, however, patches are typically heavily defoliated. Beetles can disperse long distances, and females can discern and preferentially colonize patches that are lush and lack beetle chewing damage (Herzig and Root 1996). Females can easily repopulate new patches because the majority of females mate before leaving a patch, and males tend to aggregate on patches that contain females (Herzig and Root 1996). Furthermore, Morrow et al. (1989) found that *Triirhabda canadensis* in Minnesota preferred pure host stands over more diverse vegetation. Finally, we found that the per capita stem damage on *S. altissima* increased with the density of *S. altissima* in both 1989 and 1990, the only years when data were available to test for these correlations (1989, $n = 15$, $r^2 = 0.34$, $P < 0.023$; 1990, $n = 14$, $r^2 = 0.25$, $P < 0.068$; one outlier was removed from this regression). Overall, these studies suggest that beetles will preferentially colonize the most lush and dense patches or fields of goldenrods. Although speculative, this suggests an important negative feedback mechanism of consumer regulation, whereby outbreaking specialist insects reduce the biomass and productivity in goldenrod fields, when averaged over relatively large temporal and spatial scales. Consequently, outbreaks are unlikely to be stochastic, but probably a function of previous damage, goldenrod vigor and abundance, and the current pattern.
of beetle boom and bust in the region. This mechanism can account for not only the rapid spread of goldenrods overseas, but also the existence of highly productive stands that occur in Europe and Japan, where goldenrods lack their specialist insects (Hirose 1971, Takefuji 1980, Bornkamm 1984, Guzikowa and Maycock 1986, Yoneda and Okata 1987, Weber 1994, 1997, Jobin et al. 1996). Goldenrod stands tend to have lower productivity in the United States (Melinger and McNaughton 1975, Bakelaar and Odum 1978, Carson and Barrett 1988). We suggest that this negative feedback mechanism may operate elsewhere and may not be unique to goldenrod communities.

**Outbreaking insects: a potentially potent factor influencing community regulation and plant species coexistence**

The long-standing and still-prevailing wisdom is that insect outbreaks are “generally rare and unusual events in ecosystems” (Hairston et al. 1960, Hartley and Jones 1997). We argue, however, that “rare and unusual” events must be evaluated (1) within the context of the frequency of the outbreak relative to plant life span, (2) on whether these events are related to host abundance, and (3) on the temporal and spatial scale of the defoliation caused by the outbreak.

*The case for a general role for chrysomelids in community regulation.*—We suggest that chrysomelid beetles may play a strong, yet vastly underestimated, role in plant community dynamics because of their tendency to outbreak (White 1996) and aggregate on host plants or dense host patches (Morris et al. 1996). In fact, three of the most “spectacular cases” of biological control have used chrysomelid beetles to control exotic perennial plants (*Hypericum perforatum*, *Senecio jacobaea*, and *Alternanthera philoxeroids*), and two more success stories with chrysomelids seem likely (Huffaker 1964, Maddox et al. 1971, Crawley 1989b, McEvoy et al. 1993, White 1996). We recognize there are concerns with extrapolating cases of biological control to native insects and plants (Crawley 1989b). Nevertheless, these cases suggest that native chrysomelids may play similar roles in native vegetation. The potential consequences of these outbreaks on long-lived species over large temporal and spatial scales remain little understood, even though these outbreaks have been reported.

The case for a general role for outbreaking insects in community regulation.—Outbreaks of native insects, other than chrysomelids, may also be critical to the dynamics of a number of different community types. Often, the outbreaking insect attacks the dominant species, and these attacks frequently occur repeatedly during the time a species is abundant in a stand. For example, grasshopper outbreaks can consume 50–95% of available plant biomass in prairies (Capinera 1987, Joern 1989, Chase 1996), yet the consequences of these outbreaks for community regulation remain unresolved and little studied (Joern 1989). In California coastal prairie, bush lupine (*Lupinus arboresus*) suffers extensive mortality from outbreaks of the ghost moth (*Heptalmus californicus*), causing long-term fluctuations in both lupine and competing weedy exotics (Strong et al. 1995, Maron and Connors 1996). Danell and Ericson (1990) showed that outbreaks of the antler moth (*Cerapteryx graminis*), which have been occurring for centuries, can strongly influence patterns of diversity and abundance in meadows. Spruce budworm outbreaks, which can cover millions of hectares, have occurred repeatedly over the last century, and damage tends to be more severe per capita in large pure stands of spruce (MacLean 1980, 1988, Cappuccino et al. 1998). These and other insect outbreaks can alter coniferous forest dynamics and patterns of species abundance for decades (Amman 1977, Romme et al. 1986, MacLean 1988, Veblen et al. 1991, Hadley and Veblen 1993). In tropical forests in Costa Rica, Janzen (1981) identified >20 insect species that heavily defoliated their respective host trees; he concluded that such events were “fairly common.” Overall, in many forest ecosystems, outbreaks of native insects are relatively common, widespread, and apparently have been occurring for long periods of time (Amman 1977, Schowalter et al. 1986, Nothnagle and Schultz 1987, Hadley and Veblen 1993, Bergeron and Charron 1994, Cappuccino et al. 1998). Lowman (1997) suggested that outbreaks in forests may be more common than currently recognized because they go unnoticed, out of view in the forest canopy.

The majority of theories of trophic-level regulation have paid scant attention to insect outbreaks (Hairston et al. 1960, Oksanen et al. 1981, Oksanen 1990, Strong 1992). We agree with Strong (1992) that, in some cases, herbivore effects on terrestrial plant communities may represent “trophic trickles,” but insect outbreaks seemingly represent periods of flash-flooding. If outbreaks or dense aggregations of insects sporadically defoliate the dominant plant species in the community, and if these outbreaks are more likely to occur in more lush or monospecific host stands (Root 1973, Crawley 1983, Price 1997, Cappuccino et al. 1998; but see Bach [1988a, b]), then outbreaks may be an important mechanism of community regulation (cf. Strong 1992, Polis and Strong 1996).

On the role of insect herbivores at nonoutbreak levels

Our results demonstrate that an insect outbreak could promote species richness and plant coexistence. Our data and others (see the papers by V. Brown, as well as others cited in the Introduction) also provide evidence that, even at nonoutbreak levels, insects may play a significant role in community regulation. For example, we found that suppressing insects caused an increase in stem height (Fig. 1) and sexual reproduction (see Root 1996) prior to the outbreak event in 1987. Additionally, after the outbreak, goldenrod densities never could rebound to levels in insecticide-treated plots (Fig. 1; years 1988–1990). In this regard, nonoutbreak levels of insect herbivory may act to extend the effect of an outbreak by delaying the return of the vegetation to pre-outbreak conditions. Indeed, nonoutbreak levels of insects significantly damaged goldenrods after the outbreak (Fig. 2). Additionally, when the influences of contemporaneous herbivory are factored out by comparing plant performance in plots that were sprayed for differing numbers of years, Root (1996) was able to show that low levels of herbivory can have cumulative effects on goldenrod flowering and production that continue to be expressed for ≥2 yr. Furthermore, we found that nonoutbreak levels of insects could alter the first three years of succession in three different nearby old fields (Carson and Root, in press). Finally, Carson (unpublished data) is currently finding a fairly strong influence of insect herbivory at nonoutbreak levels on three species of clonal goldenrods (*S. altissima*, *S. gigantea*, and *S. missouriensis*), across 20 grassland and old-field sites in Minnesota, USA. Overall, these results suggest that nonoutbreak levels
of herbivory may play a role in these communities, but long-term experiments (≥10 yr; cf. Gibson et al. 1990) over broad spatial scales may be required to more critically evaluate the role of insect herbivory under non-outbreak conditions (see also Huntly [1991] and Crawley [1997]).

Herbivory, insect outbreaks, and resource competition theory

Tilman and Wedin (1991) and Wedin and Tilman (1993) demonstrated that the superior competitor among common grass species in prairie was predicted by $R^*$, the level to which a species could deplete nitrogen in soil monocultures. Grover (1994, 1997; see also Holt et al. [1994]) extended the $R^*$ model by adding herbivores, in an attempt to identify assembly rules in model communities. Grover (1994) concluded that the specialist herbivores of competitively superior plants (those with low $R^*$) are keystone herbivores, when their removal allows their host plant to consume resources to levels below which other plants cannot survive. Goldenrods can form tall dense canopies of interconnected ramets that severely shade subordinate species (Carson and Pickett 1990, Bazzaz 1996). We propose that $S. altissima$ and $S. canadensis$ are the dominant clonal herbs over such a broad geographic region, because, more so than other herbaceous species, they can lower understory light to levels that displace other herbs and resist invasion (Bazzaz 1990, 1996, Carson and Pickett 1990). This is closely analogous to the way in which little bluestem ($Schizachyrium scoparium$) excludes other species by reducing soil nitrogen levels (Tilman and Wedin 1991, Wedin and Tilman 1993). In the case of goldenrods, however, insect herbivory thins dense canopies by damaging leaves, killing stems, reducing vegetative reproduction, lowering levels of belowground clonal integration, and reducing nitrogen uptake, which decreases final plant size (McCrea and Abrahamson 1985, Schmid and Bazzaz 1987, Schmid et al. 1988a, Cain et al. 1991, Brown 1994). Placed within the context of competition theory (sensu Tilman 1982, 1988; see also Grover [1994, 1997] and Holt et al. [1994]), insect herbivory delays or prevents goldenrods from reducing understory light to very low levels. This in turn promotes species diversity and plant species coexistence, and increases the rate of succession.

Herbivory and fecundity of subordinate species: a novel mechanism by which herbivores promote diversity

Insect herbivory in the canopy indirectly led to an increase in flowering in the understory (see also Danell and Ericson [1990]), most likely by increasing light availability. We found a highly significant positive linear relationship between light availability in the understory and both the flowering of $Hieracium pratense$ and the flowering of a group of understory forbs (Fig. 12). We also found a highly significant negative relationship between the log of the biomass of $S. altissima$ and both the flowering of $Hieracium pratense$ and the flowering of this same group of understory forbs (Fig. 12). These data suggest that an important mechanism by which insect herbivores might promote diversity in plant communities is by their indirect enhancement of flowering and subsequent seed rain within the community. Because the response of flowering to an increase in light availability is highly linear (Figs. 12 and 15), even a small amount of insect damage in the canopy may be sufficient to indirectly promote recruitment by seeds of subordinate species in situ. For example, Tilman (1993) found that following 11 yr of nutrient enrichment, plant species diversity declined, due to high rates of displacement of species, as well as by a decline in new species recruitment. He attributed this decline in recruitment to the accumulation of a dense litter mat (see also Carson and Peterson [1990]). Tilman (1993) did not consider that recruitment might have declined as a result of a decline in fecundity in situ by species suppressed in the understory. In subsequent experiments, Tilman (1997) added the seeds of 54 species to grassland plots and found that these communities were strongly recruitment limited. In our study, some of the understory species do not have long-lived seeds (e.g., $Daucus carota$), but are able to establish from seed within intact vegetation (Gross and Werner 1982, Gross 1984). A loss of within-community seed production would likely lead to a loss of these species within the community (Gross 1984). Consequently, even if insects only cause a small amount of damage to the overstory when they are at low abundance, this damage may help maintain higher levels of flower and seed production of nonhost species and, therefore, higher levels of species recruitment. The indirect effects of herbivores on enhancing seed production of nonhosts has received little consideration in reviews (Hendrix 1988, Louda et al. 1990, Gange 1990, Marquis 1992, Crawley 1997, Oliff and Ritchie 1998), but may be operating even when insects cause only small amounts of damage to plant canopies. This mechanism may be most important in highly productive vegetation characterized by dense canopies (e.g., tropical rain forest), where even a small increase in light in the understory may be especially critical to the reproduction of understory taxa.

Conclusions

We have reported the results of a 10-yr insect exclusion study, where an outbreak of a chrysomelid beetle had a major long-term impact on old-field community dynamics, standing crop biomass, structure, composition, species richness, and species fecundity. We argued that such outbreaks may be extremely important in community dynamics, but for the most part are ignored in theories of community regulation. The fact that (1) native phytophagous herbivores periodi-
cally irrupt and reduce the abundance and vigor of dominant plant species, (2) that these outbreaks may occur more readily in dense or lush concentrations of their hosts, and (3) that an outbreak may occur more than once during the life span of a long-lived host suggests that outbreaks may be important in community regulation and deserve serious attention from experimentalists and theorists alike.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation (NSF) grants BSR-8817961 and BSR-95 27536 and by Hatch Project 410 to R. B. Root. W. Carson was supported by NSF grants DEB-95 27729 and DEB-95 15184 during manuscript preparation at the University of Pittsburgh. We thank Anthony Bledsoe, Jon Chase, Rachel Collins, Anthony Joern, Zac Long, Peter Marks, Peter Morin, Mandy Raab, Evan Siemann, Henry Stevens, and Sara Via for comments on various drafts of the manuscript. Doug Deutschman, Charles McColluch, Kirk Moloney, and Henry Stevens helped with statistical analyses. Amy Kaufman helped prepare all of the figures. We owe a huge thanks to Greg Bartus who assisted with the study during three key field seasons. Tom Dayton, Tom McGowan, Chris Peterson, and especially Mandy Raab pitched in during several busy periods.

LITERATURE CITED


SAS Institute. 1997. SAS/STAT Software: changes and en-


