The Effects of Low-Level Consumption by Canopy Arthropods on the Growth and Nutrient Dynamics of Black Locust and Red Maple Trees in the Southern Appalachians

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THE EFFECTS OF LOW-LEVEL CONSUMPTION BY CANOPY ARTHROPODS ON THE GROWTH AND NUTRIENT DYNAMICS OF BLACK LOCUST AND RED MAPLE TREES IN THE SOUTHERN APPALACHIANS[1]

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Abstract. The effects of low-level consumption by canopy arthropods on foliage nutrient content, canopy leachates (throughfall), and biomass of 4-yr-old black locust (*Robinia pseudoacacia*) and red maple (*Acer rubrum*) were studied in the southern Appalachians of North Carolina. A carbaryl insecticide was used to reduce foliage consumption from ≈10 to ≈2% in black locust and from ≈4 to ≈1% in red maple.

Phosphorus concentrations in untreated black locust foliage were significantly lower than those of insecticide-treated foliage early in summer, but equalled concentrations of treated foliage by late summer. Potassium concentrations in untreated red maple foliage were significantly reduced during late summer; calcium concentrations in untreated red maple foliage were significantly higher later in the summer.

Potassium in throughfall from black locust trees (amount of K collected below the canopy minus bulk precipitation inputs) increased from 5.7 kg/ha for insecticide-protected trees to 9.8 kg/ha for unprotected trees ($P < .05$). Potassium losses from unprotected red maple also increased. Black locust lost 0.3 kg/ha of sulfate-S from untreated trees, but adsorbed 0.4 kg/ha of sulfate-S in insecticide-treated trees ($P < .05$).

Total biomass production (net primary production per kilogram of preseason biomass) was unaffected by the low levels of herbivory observed here. Such nominal herbivory did not stimulate biomass and nutrient accretion by these tree species but did increase the cycling of K and perhaps other elements within these systems.

Key words: Acer rubrum; arthropods; canopy; Coweeta; elements; herbivory; North Carolina; nutrients; Robinia pseudoacacia; throughfall.

INTRODUCTION

The role of canopy arthropods in the nutrient dynamics of forested ecosystems continues to be a subject of interest and controversy (e.g., Mattson and Addy 1975, Schowalter 1981). Does moderate grazing benefit trees, as suggested for other plant forms (e.g., McNaughton 1979, Detling et al. 1980)? Canopy arthropod consumers have many direct and indirect effects on plant growth and nutrient cycling processes (e.g., Kimmins 1972, Mattson and Addy 1975, Nilsson 1978, Chapin and Slack 1979, Zlotin and Khodashova 1980, Hilbert et al. 1981, Schowalter et al. 1981, Dyer et al. 1982). Extensive herbivory (partial or total defoliation) is known to decrease wood production (Rafes 1970, Morrow and LaMarche 1978), may temporarily increase litterfall (Kimmins 1972) and thereafter decrease litterfall (Nilsson 1978), and can greatly increase the amount of elements lost via canopy leaching (Kimmins 1972, Nilsson 1978). These results included comparisons of trees or forests experiencing extensive herbivory to those systems experiencing moderate or low levels of consumption by canopy arthropods. Nominal (low-level) consumption effects have therefore been included in the "controls" of defoliation studies, and the impact of nominal consumption on forest processes has received little direct study. Low-to-moderate levels of herbivory are believed by some to stimulate nutrient cycling processes and may therefore benefit plant growth by increased availability of such elements as N, P, or K (Rafes 1970, Reichle et al. 1973, Mattson and Addy 1975, Owen 1978, Schowalter et al. 1981). However, direct evidence supporting this hypothesis is lacking. In the present study we used an insecticide to reduce nominal consumption of tree foliage by canopy arthropods to very low levels. Comparisons of nutrient content, biomass production, and nutrient losses were made between insecticide-treated and untreated black locust (*Robinia pseudoacacia*) and red maple (*Acer rubrum*). We tested the general hypotheses that nominal herbivory stimulates nutrient cycling, and that these processes, in turn, benefit the plants experiencing nominal herbivory.

SITE DESCRIPTION

Research was conducted on watershed 7 of the Coweeta Hydrologic Laboratory in the southern Appalachians of North Carolina, in an area formerly oc-

cupied by a mesic oak-hickory forest that was clear-cut in 1977. The vegetation on this site was initiating its 4th yr of growth following cutting. First-year response of this vegetation following clear-cutting has been described by Boring et al. (1981), and readers are referred to that study for details of soils, topography, and site history. Schowalter et al. (1981) reported on the numbers and trophic status of the canopy arthropods found on this watershed during the 1st and 2nd year following cutting. Foliage consumption by chewing insects was estimated at only 2.7% of plant biomass; however, indirect calculations of consumption by chewing and sucking insects produced an estimate of ≈20% of net primary production.

The canopy of this regrowth forest was largely closed when this research began. Trees used in this study averaged 4 m in height at the beginning of the growing season. Vigorous regrowth by stump sprouts, accompanied by rapid growth of such species as black locust and wild grape (*Vitis* spp.), were responsible for the rapid recovery of plant biomass following clear-cutting (Boring et al. 1981).

Black locust and red maple trees were selected for study because of their dominance in the regrowth forest, and because the two species exhibited very different life history characteristics. Red maple will remain abundant in this forest through time, while black locust will become much less important as the forest approaches maturity (Day and Monk 1974, Boring et al. 1981). Moreover, the nutrient content of these two species differed markedly, particularly in N and K content (Boring et al. 1981). Thus, we speculated that these two trees might respond differently to varying levels of herbivory.

METHODS

Tree growth and canopy arthropod consumption

Trees were selected for study prior to the initiation of growth in 1980. Twelve black locust trees and 12 red maple trees (each of the latter consisting of clumps of stems emerging from a single stump) were identified, and all stems ≥5 mm in diameter 40 cm above the ground were marked and measured. Attempts were made to select trees of equal size and with equal numbers of stems; in fact trees varied in both size and number of stems. Treatments were assigned to trees randomly.

Preseason and postseason stem diameter measurements were used to calculate biomass and net primary production. A series of allometric equations, specific for each tree species and for a given range of stem diameters, were used to estimate wood and foliage biomass (Boring et al. 1981, and L. R. Boring, *personal communication*). Biomass and NPP estimates were divided by the estimate of preseason wood biomass for each tree. This procedure corrected biomass estimates for initial variation in tree size between treatments.

Foliage consumption was estimated on the basis of leaf area removed by arthropods. Four medium-sized branches (stem diameters of 1–2 cm) were removed from each tree once in June, once in July, and once in August. Two branches were obtained from the top of the canopy and two were removed from the lower portion of the canopy. Foliage therefore consisted of both sun and shade leaves, and, as new foliage was produced on all trees throughout the summer, leaves of variable age. Every other leaf (or leaflet for black locust) was removed from these branches and placed in a plant press (a total of ≈40 red maple leaves or 100 locust leaflets per tree). Leaves were returned to the laboratory and photocopied, then dried and saved for nutrient analysis. A computerized polar planimeter was used to measure the area of each leaf photocopy and the areas removed by chewing insects (photocopies showed <0.1% distortion). Leaves missing tips or edges were assumed to be symmetrical and/or have the same shape as other leaves in the sample. Consumption per tree was defined as the area removed divided by the total area measured. This procedure may overestimate consumption by chewing insects (Reichle et al. 1973), but does not include estimates of consumption by sucking insects. We used a single tree rather than a single leaf as the sample unit to avoid biases caused by different leaf areas measured per tree.

Nutrient analysis of foliage and throughfall

Elemental concentrations of Ca, K, Mg, and P in foliage were measured with a dry ash procedure followed by analysis using plasma emission spectroscopy. Standard reference material (United States Bureau of Standards' orchard leaves) was used to monitor accuracy and correct for incomplete recovery of such elements as P. A micro-Kjeldahl procedure was used to measure N content of foliage. Leaf petioles were included in the analyses of red maple but were not included in the analyses of black locust.

Throughfall collections were made with 15 × 200 cm V-notch troughs placed directly beneath each of the 24 trees. The advantages of using long troughs rather than funnel collectors have been noted by Best and Monk (1975). Variations due to differences in leaf area or to uneven movements of water through the canopy are reduced with this type of collector. Troughs were elevated 40 cm above the ground to eliminate soil splash contamination, and were covered with 1-mm fiberglass mesh windowscreen to exclude macroparticulates. All vegetation other than that of the study tree was removed for several metres above and around the troughs. Throughfall was collected following each rainfall event, and the volume of throughfall was recorded for each collector. One millilitre of phenyl mercuric acetate was added to each collector to reduce microbial activity. Samples were stored at 4°C until pooled into a single sample representing 1 mo of throughfall. Stemflow, which may be affected by can-

TABLE 1. Estimates of leaf area consumed by chewing insects. Data are means of six samples per treatment. Each sample consisted of ≈40 maple leaves or 100 black locust leaflets.

| Species | Treatment | Leaf area removed (%) (mean and range of observed values) | | |
		June	July	August
Black locust	Untreated	5.3 (3.1–13.1)	13.2* (8.5–17.5)	10.5* (9.5–15.9)
	Insecticide-treated	2.7 (1.2–4.1)	2.4 (0.4–6.5)	1.7 (0.6–3.0)
Red maple	Untreated	3.4 (1.6–6.3)	no data	4.4* (1.6–10.9)
	Insecticide-treated	1.9 (0.6–5.7)	no data	1.3 (0.3–3.8)

* Significantly greater than paired value ($P < .05$; test performed using arcsine-transformed data).

opy arthropod consumption (Nilsson 1978), but which likely contains <10% of elements lost from the canopy (Carlisle et al. 1967), was not collected.

Estimates of bulk precipitation inputs (elements in rainfall and dryfall) were obtained from a monitoring network of six collectors maintained by United States Forest Service personnel at Coweeta. Average concentrations of elements from these collectors were multiplied by the average amount of rainfall obtained from two rain gauges located on either side of the study area. Thus, data presented here on bulk precipitation inputs are specific to the study area and may differ slightly from estimates made for the entire Coweeta Basin. Nutrient content of bulk precipitation and total throughfall (bulk precipitation and canopy leachates) were measured using atomic absorption spectrophotometry for cations. Nitrogen species and anions were measured colorimetrically with autoanalyzer procedures.

The amounts of elements in throughfall can be calculated by multiplying elemental concentrations by the volume per collector. These direct measurements were not always possible, however, due to occasional overflow of collectors or to leakage problems. The amount of precipitation retained by the forest canopy has been intensively studied at Coweeta, and the amount and type of foliage does affect throughfall volumes (Helvey and Patric 1965, Best and Monk 1975). Throughfall volumes were therefore estimated from regression equations using data obtained from about half of the rain events (i.e., from events where overflow or leakage did not occur in any of the collectors). Equations were developed for each species for trees with similar stem diameters (three equations for black locust, two for red maple). Correlation coefficients for these regressions equalled or exceeded values of .97.

Insecticide treatment

Half of the black locust and red maple trees were treated with carbaryl (1-naphthyl N-methyl carbamate, liquid Sevin) twice monthly or more frequently if any insect activity was noted. Spraying was initiated

in early May, 1–2 wk after leaf bud-break. Care was taken only to mist the trees, thereby avoiding additional leaching losses. Carbaryl ($C_{12}O_2NH_4$) added ≈0.5–1 g of N per month to the foliage of each sprayed tree. Throughfall troughs were covered during spraying to avoid direct contamination; however, the treatment may have caused a fertilization effect and/or affected N concentrations in foliage tissue and in canopy leachates. Thus, the N data presented here must be interpreted with caution.

Potential indirect effects of the insecticide and canopy arthropods

Foliage consumption has been reported to cause early leaf drop in certain plant species (Dixon 1971, Owen 1978). We tested this possibility by placing 0.4-m² litterfall traps, fitted with 1-mm windowscreen mesh, at the base of six insecticide-treated trees and six untreated trees. Litterfall was collected twice between May and August, dried, and weighed.

We also recognized that the insecticide might affect forest floor detritivores (Stegeman 1964), or that canopy arthropod feeding activities might stimulate forest floor decomposition and mineralization processes (e.g., Zlotin and Khodashova 1980). We therefore measured the rate of decomposition of senescent dogwood (*Cornus florida*) leaves beneath treated and untreated trees. Leaves were placed in litter bags and weighed following the procedure of Seastedt and Crossley (1980). Forty bags were placed under the trees in late April, and all were harvested on a single date in September. This procedure was used only to evaluate potential treatment effects on decomposition processes; it did not measure the actual decomposition rate of litter beneath these tree species.

RESULTS

Arthropod consumption of foliage

The leaf area consumed by chewing insects was significantly reduced by insecticide application (arcsine transformation of percentage of leaf area removed, $P <$ .05, Table 1) from ≈10 to ≈2% in black locust and

TABLE 2. Effects of insecticide treatment and sampling date on nutrient concentrations of foliage. Concentrations are averages of 36 samples per treatment (two replicates per tree per month, June through August).

Element	Concentration (mg/g)		F value (Type IV ss)†	
	Un-treated	Insec-ticide-treated	Treatment (1 df)	Date (2 df)
		Black locust		
N	31.3	32.4	2.94	1.39
P	1.8	2.0	12.59**	33.90***
K	15.3	15.7	0.62	6.93**
Ca	7.4	7.7	0.07	3.93*
Mg	2.7	2.5	0.81	2.38
		Red maple		
N	17.6	17.4	0.04	11.08***
P	1.4	1.4	0.05	10.13***
K	8.0	9.1	7.13*	6.15**
Ca	6.9	5.9	5.78*	19.28***
Mg	2.2	2.2	0.01	6.92**

† No significant interaction between treatment and date was observed for any of the elements.
* $P < .05$, ** $P < .01$, *** $P < .001$; ANOVA.

from ≈4 to ≈1% in red maple. Consumption by sucking insects is believed to be equal to or greater than that of chewing insects at Coweeta (Schowalter et al. 1981); hence, actual consumption percentages may be double those presented in Table 1.

Concentrations of N and Mg in foliage of both tree species were unaffected by the insecticide treatment (Table 2). The average concentration of P in black locust foliage was higher for insecticide-treated trees, while insecticide-treated red maple foliage averaged higher K concentrations and lower Ca concentrations than untreated foliage. Phosphorus concentrations in untreated black locust foliage were significantly lower early in the growing season; however, concentrations eventually equalled those of insecticide-treated foliage (Fig. 1). Assuming no foliar biomass differences (see below), these results suggest replacement of lost P in untreated foliage or belated losses of P in treated foliage. Differences between treatments in foliage concentrations of K and Ca of red maple became apparent later in the growing season (Fig. 2). Potassium differences are assumed to be the result of enhanced leaching losses of K from herbivore-injured tissue (e.g., Tukey 1970) without a compensatory increase in K inputs to foliage. Calcium is a structural element of foliage that tends to increase in concentration over the growing season (e.g., Day and Monk 1977), but we do not know why higher calcium concentrations occurred in untreated foliage.

Arthropod effects on tree biomass and net primary production

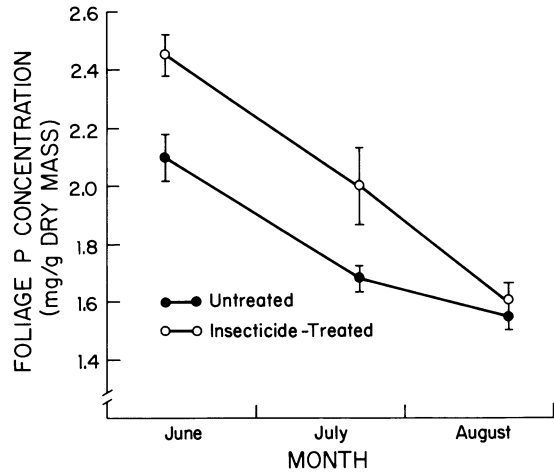Average initial tree size used in the black locust studies was identical between treatments; however,

FIG. 1. Phosphorus concentrations of insecticide-treated and untreated black locust foliage. Values are means of six trees per date, with standard errors indicated by the bars.

insecticide-treated red maples were, on the average, smaller than the untreated trees (Table 3). Comparisons between treatments were therefore made on the basis of initial stem biomass of the individual trees. The insecticide treatment had no significant effect on total production for either species (Table 3). Red maple trees subject to herbivory (untreated) did produce significantly more woody plant material per kilogram of preseason biomass; however, we cannot attribute this response solely to the levels of herbivory observed here. Instead, growth rates appear related, in part, to the initial size of the trees. As these trees were
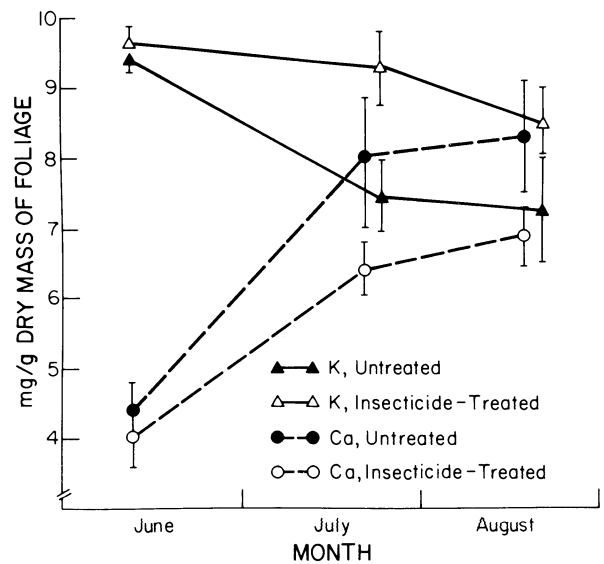

FIG. 2. Concentrations of K and Ca in insecticide-treated and untreated red maple foliage. Values are means of six trees per date, with standard errors indicated by the bars.

TABLE 3. Biomass and net primary production of insecticide-treated and untreated black locust and red maple. Values are means of six trees per treatment; standard errors are in parentheses.

Species	Treatment	Preseason stem biomass (kg)	Postseason stem biomass (kg)	Woody growth per stem* (kg/kg)	Foliage production (kg)†	Foliage production per stem (kg/kg)	NPP per stem (total) (kg/kg)
Black locust	Untreated	3.70 (0.70)	6.88 (1.46)	0.85 (0.09)	1.85 (0.29)	0.53 (0.05)	1.38 (0.13)
	Insecticide-treated	3.66 (0.33)	7.46 (0.72)	1.11 (0.17)	1.79 (0.16)	0.51 (0.04)	1.62 (0.19)
Redmaple	Untreated	6.30 (1.12)	9.46 (1.64)	0.52 (0.05)	3.82 (0.51)	0.67 (0.06)	1.18 (0.09)
	Insecticide-treated	4.40 (1.85)	6.07 (2.54)	0.36 (0.05)	2.73 (1.04)	0.67 (0.04)	1.02 (0.06)

* New growth/preseason biomass.
† Foliage production includes the increment lost to herbivory (August consumption estimates from Table 1).

all the same age, smaller trees had a previous history of slower growth, and these trees would likely grow more slowly during the year of study as well. In support of this interpretation, the three largest treated red maple trees averaged 0.43 kg of new woody growth per kilogram of preseason biomass, while the three smallest treated maple trees averaged only 0.27 kg of new woody growth per kilogram of preseason biomass.

The growth increments of both species are sufficiently large to suggest that the application of 4 g of N in the insecticide per tree over the growing season would not be measurable as a fertilizer effect or appreciably increase foliar N concentrations.

Throughfall

Leaves injured by herbivores are known to be more susceptible to leaching of elemental constituents (e.g., Tukey 1970, 1980). Our interests centered on whether these losses had a measurable impact on the nutrient budget of this regrowth forest. The amounts of most elements in throughfall did not show measurable in-

creases due to increased herbivory (Table 4). Significant differences between treatments of black locust were, however, noted for K and sulfate-S. Potassium losses were larger beneath untreated trees (Fig. 3). Net throughfall losses of K increased with the age of the foliage; treatment differences showed no seasonal trends. Untreated foliage lost 78% more K in May, 38% more in June, 53% more in July, and 76% more K in August than did insecticide-treated foliage.

Sulfur dynamics in throughfall of black locust were markedly different from those of K in that leaching losses were highest early in the season; thereafter losses were near zero, or net gains of sulfate-S occurred (Fig. 3). Insecticide-treated foliage acted as a net sink of sulfate-S, removing slightly over 10% of the bulk precipitation input. In contrast, untreated trees were a net source of sulfate-S, contributing ≈7% over the bulk precipitation input.

Comparisons of treated and untreated red maple trees were complicated by the difference in tree size between treatments. The smaller insecticide-treated trees lost smaller amounts of elements, as expected. On the

TABLE 4. Total amounts of elements in bulk precipitation and net throughfall, May through August 1980. Net throughfall is total leachates collected beneath the canopy minus bulk precipitation inputs. Nitrogen species, PO₄, and SO₄ are expressed as kilograms of N, P, and S per hectare, respectively. Values are means of six samples per treatment, with standard errors in parentheses.

Source	Treatment	NO₃	NH₄	Organic N	PO₄	K	Ca	Mg	Na	SO₄
					Amount of nutrient element (kg/ha)					
Bulk precipitation		1.18	1.07	0.83	0.030	0.82	0.81	0.17	0.32	3.84
Net throughfall										
Black locust	Untreated*	−0.49 (.03)	−0.26 (.08)	0.60 (.25)	0.013 (.007)	9.79 (.91)	1.06 (.30)	0.64 (.14)	−0.07 (.01)	0.26 (.08)
	Insecticide-treated	−0.47 (.07)	−0.36 (.07)	0.50 (.15)	0.011 (.004)	5.72 (.33)	1.25 (.25)	0.72 (.12)	−0.05 (.02)	−0.40 (.10)
Red maple	Untreated	−0.61 (.05)	−0.71 (.04)	0.51 (.18)	0.001 (.002)	2.21 (.39)	1.13 (.09)	0.32 (.02)	−0.06 (.01)	0.19 (.18)
	Insecticide-treated	−0.39 (.02)	−0.53 (.06)	0.28 (.14)	0.001 (.001)	0.58 (.18)	0.71 (.14)	0.17 (.03)	−0.02 (.01)	−0.15 (.13)

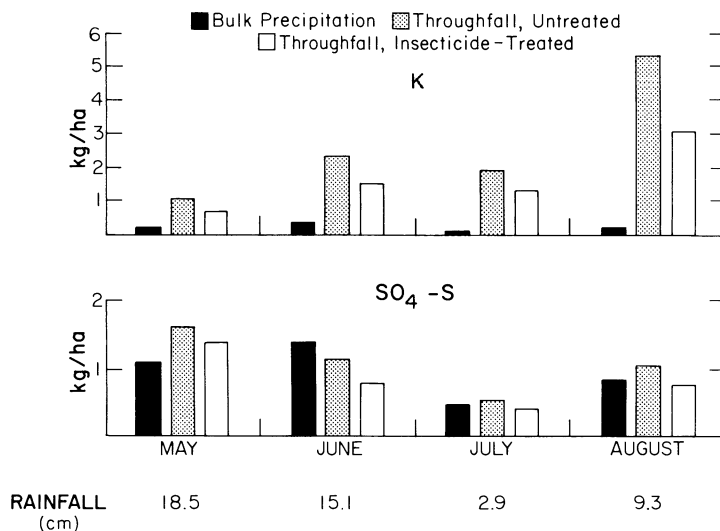* Sample size = 5 for untreated black locust.

FIG. 3. Amounts of K and SO_4-S in bulk precipitation and throughfall of black locust. The amounts of elements in throughfall include those amounts added by bulk precipitation. Amounts are means of six samples per month, except for July, where $n = 5$ for untreated trees.

basis of losses per kilogram of foliage, only K in throughfall was significantly different between treatments.

Early leaf drop and litter decay

Early litterfall was not significantly greater beneath those trees experiencing a higher level of herbivory (Table 5). Adjustments for variation in foliage biomass among trees did not change this. Perhaps most of the biomass consumed by insects was converted to small fecal pellets, which would not be collected by the litterfall traps.

Decay of dogwood litter beneath treated and untreated trees also showed no treatment effect. Dogwood litter lost 36 and 37% of its initial mass beneath treated and untreated black locust trees, respectively, and 34 and 35% of initial mass beneath treated and untreated red maple.

DISCUSSION

Interpretations of these results are based on three assumptions: (1) the insecticide did not have any direct effect on plant growth and nutrient dynamics, (2) the insecticide did not affect litter decomposition and mineralization processes, and (3) the regressions used to predict wood and foliage biomass, developed from trees experiencing low levels of herbivory, were valid for insecticide-treated trees (i.e., the ratio of stem biomass to foliage biomass was not increased by reduced herbivory). These assumptions seem reasonable. No phytotoxic effects of Sevin have been reported for these tree species, (e.g., Kuhr and Dorough 1977) and the insecticide did not appear to have a fertilizer effect (e.g., Tables 2 and 3). The insecticide also did not

affect the decomposition of dogwood litter placed beneath sprayed trees. If reduced herbivory resulted in proportionally more carbon allocation to woody tissues, then results presented for foliar biomass of insecticide-treated trees (Table 3) are overestimates. Such a bias would have to be relatively large (i.e., larger than the consumption estimates for the respective tree species) to affect results.

We recognize that the methods used in this study may have been too imprecise to detect subtle changes in plant growth and nutrient dynamics caused by low-level herbivory. For example, large standard errors in our throughfall results (Table 4) may have obscured potential herbivore-related losses of N, PO_4, and Na. However, the summer throughfall contributions of these elements to the annual nutrient budgets of forests are minimal (e.g., Carlisle et al. 1967, Best and Monk 1975). Hence, errors of this type, if present, do not seriously impair interpretations of low-level herbivore impacts on the biogeochemistry of forested ecosystems. Certain plant responses to herbivory may be delayed or cumulative (Mattson and Addy 1975, Morrow and LaMarche 1978, Swank et al. 1981), and we may be underestimating the effects of nominal herbivory on plant processes by discussing only those responses observed in a single growing season. Potential delayed responses are mentioned below; we believe, however, that we have detected the major effects of low-level or background herbivory on tree productivity and nutrient cycling processes.

Does nominal herbivory stimulate nutrient cycling in forests? A generalization will not suffice; each ion exhibited a unique behavior that was mediated to varying degrees by plant-consumer interactions.

Potassium was the only cation strongly affected by herbivory. A significant reduction in K concentrations of red maple foliage was noted later in the growing season. Losses, presumed to be caused by increased leaching of injured tissue (Table 4), were not entirely replaced by additional inputs from roots. However, the relative difference in foliar K concentrations was small ($\approx$ 10–20%), while the amount of K in throughfall for untreated trees was double that of insecticide-treated trees. As K in throughfall accounts for over half of all K cycled in deciduous forests (e.g., Carlisle et al. 1966, Cromack and Monk 1975, Whittaker et al. 1979), the actual rate of K cycling was likely increased by the small increase in herbivory. This conclusion is particularly clear for black locust, which experienced a 70% increase in net throughfall losses due to increased herbivory, without a significant reduction in foliar biomass or foliar K concentrations. Only very small amounts of K in throughfall are immobilized by litter microflora (Seastedt and Crossley, in press); hence, canopy leachates may be immediately reabsorbed by roots.

The large increase in the rate of cycling of K was not observed for other elements. This may be related to the high mobility of the K ion; however, Na, which is believed to be more mobile than K (Whittaker et al. 1979, Seastedt and Crossley 1981), was not affected by the levels of herbivory observed in this study. Sodium concentrations were too low and too variable in foliage for herbivory to have a measurable effect. Again, our interpretations are weakened by the fact that a small amount of herbivory did occur in insecticide-treated foliage, and leaching losses may be non-linear with respect to the level of herbivory. However, the relatively large differences observed for K (in terms of both absolute amounts and the ratio of treated : untreated), compared with the small differences observed for other elements, indicates that throughfall losses of these elements were not strongly regulated by the levels of herbivory observed in this study.

The June losses of P in untreated black locust foliage (Fig. 1) were likely caused by large numbers of aphids and other homopterans that preferentially feed on black locust (Schowalter et al. 1981). Chapin and Slack (1979) reported increased root uptake of P in response to moderate defoliation of tundra graminoids. If black locust roots respond similarly, then the convergence of foliar P concentrations in treated and untreated trees later in the growing season is explained. This interpretation implies more rapid cycling of P in trees experiencing moderate herbivory. However, we did not measure P content of early leaf drop nor did we measure organic P content of throughfall; thus, results remain inconclusive.

The rate of N cycling was unaffected by herbivory. Unlike K, any losses of N from trees via throughfall, frass production, or early leaf drop would not be immediately available for root uptake. The inorganic

TABLE 5. Early leaf drop (May through August) by black locust and red maple trees. Data are averages of three collectors, with standard errors in parentheses.

Species	Treatment	Litterfall	
		g/m^2	$g \cdot m^{-2} \cdot kg^{-1}$ foliage
Black locust	Untreated	132.0 (18.0)	65.3 (16.2)
	Insecticide-treated	112.3 (22.8)	59.5 (5.8)
Red maple	Untreated	38.8 (2.5)	7.3 (0.6)
	Insecticide-treated	32.0 (0.3)	13.1 (7.7)

forms of N would likely be immobilized by litter and soil microflora (e.g., Swank et al. 1981, Day 1982), while organic N must first be mineralized before it is available to plants. Enhanced root uptake of N from herbivore-mediated sources therefore would not be evident until the following growing season. Thus, herbivores may increase N cycling in forests in spite of the fact that no differences were observed in this study.

The one other element lost in significantly greater quantities by untreated black locust was sulfate-S. The S cycle is poorly known due to difficulties measuring the various solid, liquid, and gaseous phases of this element. Adsorption of gaseous S species may have influenced the pattern of throughfall losses and gains reported in Fig. 3 (e.g., Likens et al. 1977). Results from a northern hardwood forest (Whittaker et al. 1979) indicate that S dynamics, excluding gaseous fluxes, are similar to K dynamics in that the major flux of S from the canopy is in throughfall. Other investigators (e.g., Killingbeck and Wali 1978) have reported deciduous forests to be seasonal sinks for SO_4. In our study, nominal canopy arthropod consumption changed the canopy from a seasonal sink for SO_4 to a net source of SO_4. Without knowledge of tissue concentrations of this element, we cannot state that the absolute rate of S cycling was increased by herbivory. Our results do suggest, however, that the level of herbivory may influence response of a forest to inputs of SO_4 from natural and anthropogenic sources such as acid rain.

Does nominal herbivory benefit the trees experiencing the herbivory? The tentative answer is "no," at least with respect to those factors measured in this study. No increases in foliage production or total production resulted from the increased level of herbivory experienced by untreated trees. Increased herbivory did not affect wood production in black locust, while results for red maple are obscured by initial differences in tree size between treatments. Mattson and Addy (1975) suggested that herbivory could shift carbon allocation from wood to foliage, and Morrow and LaMarche (1978) demonstrated that chronic herbivory can reduce woody growth. Thus, the higher wood production in untreated red maple trees was probably not

related to the increased level of herbivory. Conversely, the levels of herbivory observed in this study did not adversely affect any growth parameter, a finding consistent with earlier reports (e.g., Rafes 1970).

Our results suggest that nominal herbivory has little, if any, role in the biomass and nutrient accretion of successional forests. The major impact of nominal herbivory is to increase the rate of cycling of K and perhaps other elements in this ecosystem.

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