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Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas-fir in western Oregon

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ABSTRACT

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We tested the effect of defoliating and sap-sucking phytophages on young Douglas-fir at the H.J. Andrews Experimental Forest in western Oregon. Experimental trees were subjected to manipulated abundances of a sap-sucking insect at 0–1 insect g^{-1} foliage or a defoliating insect at 0–0.06 g^{-1} foliage. Tree mass, throughfall, litterfall, litter decomposition, and N, K and Ca turnover were measured for each tree over a 3 year period.

Herbivore abundance had no effect on calculated tree growth or nutrient content. These data suggest compensatory growth and replacement of lost nutrients. Herbivory also did not significantly affect decomposition rate for exogenous Douglas-fir needle litter.

Throughfall volume, N, K and Ca content, and litterfall mass were positively related ($P<0.05$) to defoliator abundance during the early growing season (April–June). At the highest defoliator abundance (causing about 20% foliage removal), turnover of N, K and Ca amounted to 15–25% of the total inputs to litter during this period. Throughfall Ca was significantly related to defoliator abundance for the entire growing season (April–September). Sap-sucker feeding significantly influenced K turnover during the growing season.

The results of this study support results from an eastern deciduous forest. Our study relates nutrient turnover rates to herbivore abundances, a prerequisite for modeling phytophage effects on nutrient flows.

INTRODUCTION

Phytophages influence nutrient cycling in forest ecosystems through effects on plant growth, foliage loss, and litter decomposition (Mattson and Addy, 1975; Parker, 1983; Seastedt and Crossley, 1984; Dyer, 1986; Schowalter et al., 1986). However, despite considerable effort to suppress forest 'pests', her-

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bivore effects on nutrient cycling, which may contribute to long-term forest health and productivity (Schowalter and Crossley, 1987; Alfaro and MacDonald, 1988), remain poorly known.

Few studies have addressed herbivore effects on nutrient cycling. Kimmins (1972) introduced sufficient sawfly larvae to remove most 1-year-old foliage from young red pines and observed a significant increase in turnover of ^{134}Cs (a K analog) via throughfall leaching and defoliation. Swank et al. (1981) reported that 30% defoliation of mixed hardwood watersheds increased nitrate export. Seastedt et al. (1983) used carbaryl to reduce foliage removal from 4–10% to less than 2% on young black locust and red maple and found a consequent reduction in K, and perhaps P, turnover but no apparent effect on plant growth or litter decomposition over a 1 year period.

These studies demonstrated that phytophages can influence nutrient turnover. However, none provided data on phytophage abundances necessary for modeling effects on turnover rates. Furthermore, these studies did not address the potentially different effects of phytophage functional groups, e.g. sap-suckers vs. defoliators, which exploit the host in different ways. Our objective was to test the effects of herbivore density and functional group on primary production, nutrient turnover, and litter decomposition of young Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in western Oregon.

MATERIALS AND METHODS

Site description

This study was conducted from July 1983 to June 1986 at the H.J. Andrews Experimental Forest Long Term Ecological Research (LTER) Site, a 6100 ha facility in the central western Cascades in Oregon (latitude 44°N, longitude 122°W). The Andrews Forest is jointly operated by the USDA Forest Service Willamette National Forest and Pacific Northwest Research Station and by Oregon State University. Elevation ranges from 500 to 1500 m. A maritime climate prevails, with wet, relatively mild winters and dry, warm summers. Average annual temperature is 7.9°C; average annual precipitation is 2400 mm, with 75% occurring as rain between November and March.

Watershed 10 covers 10 ha at the western boundary of the Andrews Forest. Elevation ranges from 430 to 670 m with slope gradients of 25–50%. This watershed was the site of extensive nutrient cycling research before clearcutting and replanting with Douglas-fir in 1975 (Grier and Logan, 1977; Sollins et al., 1980) and for the first 3 years of regeneration (Gholz et al., 1985). When this study started in 1983, the conifers were 0.7–1.5 m in height.

Experimental treatments

Sixty Douglas-fir within a 1 ha area on a north-facing slope were selected for study. We selected trees showing similar crown geometry, foliage color and density, absence of prior deer browsing, and relative isolation from surrounding vegetation. These criteria minimized uncontrolled effects of variation in tree form or physiology and inputs from surrounding vegetation on measured tree growth, throughfall, litterfall, and litter decomposition.

The trees were numbered in May 1983 and randomly assigned to six experimental treatments: (1) unmanipulated phytophage abundance, (2) phytophage exclusion, (3) low sap-sucker abundance, (4) high sap-sucker abundance, (5) low defoliator abundance, and (6) high defoliator abundance. Each tree received the same treatment for 3 years (1983–1986). These treatments were designed to compare effects of phytophage functional group and abundance on nutrient flows. The exclusion treatment constituted a control, and the unmanipulated treatment was used to test models derived from the other treatments.

Phytophages were counted biweekly. Target abundances were maintained during normal feeding periods by manually adding or removing individuals. This procedure minimized variation in herbivore abundances and also avoided possible confounding effects of insecticides (as both biocide and nutrient source) on plant growth, throughfall nutrients, or litter organisms. Mass intensities (g insects per g foliage) of herbivores could not be measured directly in the field, but we estimated mass intensities from individual masses measured in the laboratory, as noted below.

Sap-suckers were represented by the abundant Cooley spruce gall adelgid, *Adelges cooleyi* (Gillette) (Homoptera: Adelgidae). This insect was present on all study trees at the beginning of the study. It feeds exclusively on current year's foliage and can reach sufficient abundance (more than $10\ g^{-1}$ foliage) to cause severe needle necrosis (Schowalter, 1989). We maintained a range of experimental abundances from less than $0.5\ g^{-1}$ foliage in the low treatment to more than $0.5\ g^{-1}$ in the high treatment. All other phytophages were removed manually from these trees. Adelgids collected from a separate set of trees were used to increase numbers on experimental trees and to estimate mass intensities after drying at 50°C.

Defoliating phytophages are infrequent (less than $1\ kg^{-1}$ foliage) in young conifer stands at the Andrews Forest (Schowalter, 1989). The silver-spotted tiger moth, *Lophocampa argentata* (Packard) (Lepidoptera: Arctiidae), was selected as a representative defoliator. This species feeds only on previous years' foliage. Colonies of second-instar larvae were collected during autumn and introduced onto treatment trees at less than $0.03\ g^{-1}$ foliage in the low treatment and more than $0.03\ g^{-1}$ in the high treatment. Other phytophages were removed manually from these trees. Additional larvae were maintained

in the laboratory to replace missing larvae, to estimate mass intensities after drying at 50°C, and to measure larval growth and consumption rates (e.g. Schowalter et al., 1977) for comparison with visual estimates of foliage removal.

Herbivores influence nutrient cycling through effects on primary production, nutrient turnover, and litter decomposition. These processes were measured for each tree as follows.

Primary production

Estimation of phytophage effect on primary production required periodic measurement of plant mass. Because experimental trees could not be killed for direct measurement of mass, foliage mass and total plant mass were estimated by regressions derived from young Douglas-fir (0.3–6.1 cm diameter at the litter surface) at the Andrews Forest (Gholz et al., 1985; M. Klopsch, unpublished LTER data, 1989). The regular growth geometry of conifers contributes to $R^2s > 0.90$ based on diameter (M. Klopsch, unpublished LTER data, 1989).

Diameters were measured at the litter surface at the beginning of the study and in April (before new foliage production) each year thereafter. Dry foliage mass in grams (Y_F) was calculated as

$$\ln Y_F = 3.8 + 1.3 \ln X \; (P < 0.0001, R^2 = 0.91)$$

where X is stem diameter in centimeters (M. Klopsch, unpublished LTER data, 1989). Change in calculated foliage mass with time provided an estimate of foliage production. Total plant mass in grams (Y_P) was calculated as

$$\ln Y_P = 4.2 + 1.6 \ln X \; (P < 0.0001, R^2 = 0.93)$$

where X is as above (M. Klopsch, unpublished LTER data, 1989). Change in calculated total plant mass with time provided an estimate of primary production.

Small (1 g) samples each of current year's and previous year's foliage were collected from mid-whorl branches from each tree in June. Each sample was analyzed for Kjeldahl N using autoanalyzer techniques, and for K and Ca using perchloric acid digestion followed by standard atomic absorption spectrophotometry, with addition of LaCl for calcium analysis. These elements are biologically important and represent the range of turnover rates in ecosystems (e.g. Sollins et al., 1980).

Nutrient turnover

Our technique for measuring nutrient turnover as throughfall leaching/stemflow (throughfall) and litterfall took advantage of conifer geometry, i.e. a conical crown oriented along the axis of the bole. Triangular, galvanized-steel pans, 8 cm deep with a 36° angle fitted to the bole, were used to collect

throughfall and litterfall (Fig. 1). Each collector was covered with sheet metal beyond the crown perimeter so that the collector intercepted only material representing 10% of the crown area. Collectors were connected by plastic tubing to a 20 l jug which stored throughfall. A 1×1 mm aluminum mesh screen was inserted into each collector to retain particulate material and prevent blockage of the drain. Throughfall was probably augmented by nutrients leached from litterfall.

Throughfall in the jugs and litterfall on the screens were collected and measured biweekly. Subsamples (1000 g) of throughfall were filtered and frozen before elemental analysis, usually within 2 weeks. Samples were analyzed for N, K and Ca, as above. This procedure was selected for the following reasons: (1) precipitation at the Andrews Forest is nearly continuous from November to April, (2) field temperatures during this period are below 10°C and limit microbial activity, (3) microbicides could confound elemental analyses, and

Fig. 1. Proportional sampler for collecting throughfall/stemflow and litterfall from 10% of the canopy of young Douglas-fir at the H.J. Andrews Experimental Forest in western Oregon.

(4) earlier field studies have indicated satisfactory results for N (Klingaman and Nelson, 1976). Microbial activity was controlled further by the use of aluminum screens and by acid washing the jugs in 1 N H_2SO_4 for 24 h and rinsing with deionized water every 6 months.

Litterfall was dried at 50°C to constant weight and pooled annually by tree for N, K and Ca analysis. Elemental concentrations were measured as above.

Three collectors were placed on exposed sites within the study area to collect raw precipitation. Precipitation volume was measured, and 1000 g subsamples were analyzed for N, K and Ca, as above. Nutrient content of precipitation was subtracted from throughfall nutrient content.

Litter decomposition

Litter decomposition rate was measured as mass loss of litter samples under each tree using 1×1 mm polyester mesh litterbags (10×10 cm) filled with 3.00 g of Douglas-fir needle litter (Fogel and Cromack, 1977). This mesh size retained needles but permitted gas exchange and movement of small invertebrates such as protozoa, nematodes, and microarthropods.

Litterfall from the study trees was insufficient; therefore, we used senescent needles shaken from mature Douglas-fir near Corvallis, Oregon, in September 1983. This exogenous needle litter and the litter from our study trees may have differed qualitatively, but we expected decomposition to be affected by canopy condition and herbivory in the study trees (Fogel and Cromack, 1977; Seastedt and Crossley, 1983).

Ten litterbags were placed under each study tree in March 1984 (Fogel and Cromack, 1977). An additional 10 litterbags were returned immediately to the laboratory for measurement of needle loss during transit. These litterbags also were used to measure initial concentrations of N, K and Ca, as above. Subsequent subsamples (two litterbags per tree) were collected after 3, 9, 15, 21 and 27 months in the field. Samples were dried at 50°C, weighed, and pooled by tree for N, K, and Ca analyses, as above.

Data analysis

Missing throughfall volumes (about 5% of the data set) resulted from collector overflow during periods of heavy precipitation and from disconnection caused by animals or slope failure. Estimation of missing data was necessary for calculation of seasonal totals. Missing values were estimated from highly significant ($P < 0.01$, $R^2 > 0.9$) linear regressions relating measured throughfall to calculated throughfall, based on precipitation and collector area, for each tree.

Variability caused by tree size was standardized by dividing by foliage mass and expressed per gram of foliage. Nutrient contents of foliage, net through-

fall, and litter were calculated by multiplying mass by elemental concentrations. The natural log transformation was used, as necessary, to linearize regression and meet assumptions of normality and constant variance.

Linear regression techniques (Steel and Torrie, 1980) were used to relate nutrient flows to manipulated phytophage abundances. The exclusion treatment served as the control for both phytophage species. Cook's D influence statistic was used to detect observations with particular influence on linear models. All analyses were performed using SAS software (SAS Institute, 1982).

Results of regressions were used to predict expected nutrient flows for the 10 unmanipulated trees. We compared measured and expected flows using regression analysis (Steel and Torrie, 1980).

RESULTS

Primary production

Mean stem diameter (± 1 SD) was 2.45 cm (± 0.70) at the beginning of this study. Calculated foliage masses of the 60 trees averaged 150 g (± 57), and total mass averaged 300 g (± 150). Trees did not differ significantly in size among treatments. Biomass of Douglas-fir foliage for this watershed during 1986 was about 1400 kg ha^{-1} (M. Klopsch, unpublished LTER data, 1989).

Average experimental abundances of sucking phytophages, *A. cooleyi*, on treated trees ranged from 0 insects g^{-1} to 1.3 g^{-1} foliage during the growing season (April–September). At 0.0071 (± 0.0072) mg per insect, mass intensities on treated trees ranged from 0 to 0.007 mg insect g^{-1} foliage. We were unable to increase abundances of this insect to higher levels (greater than 10 g^{-1}) reported for some other regenerating watersheds at the Andrews Forest (Schowalter, 1989) despite introduction of large numbers of eggs.

Average experimental abundances of defoliating phytophages, *L. argentata*, ranged from 0 to 0.06 insect g^{-1} during the early growing season (April–June). At 72 (± 2) mg per larva, mass intensities were 0–4.0 mg g^{-1}. Consumption by larvae in the laboratory averaged 2.6 g per larva. Estimated foliage loss by treated trees ranged from 4 to 20%, nominal (5–15%) for forest ecosystems (Schowalter et al., 1986), but higher than typical defoliation in young stands at the Andrews Forest (Schowalter, 1989).

Neither phytophage significantly affected diameter growth, foliage production, or total production ($P > 0.30$), nor were trends apparent over the range of experimental abundances. Stem diameter growth averaged 1.6 cm (± 0.7), or 66% of initial diameter, between April 1984 and April 1986. Foliage production averaged 140 g (± 66), or 100% of initial mass. Total production averaged 390 g (± 210), or 150% of initial mass. The substantial increase in plant mass over 2 years and the high correlation coefficients of the regressions

TABLE 1

Elemental pools in foliage and inputs to litter as throughfall and litterfall at 0 and 20% defoliation of young Douglas-fir during April–June at the H.J. Andrews Experimental Forest in western Oregon

	Mass (kg)	N (g)	K (g)	Ca (g)
Foliage pool	1.0	9.8	4.5	3.7
Throughfall (no defoliation)	240	0.025	0.079	0.038
Litterfall (no defoliation)	0.0068	0.065	0.012	0.038
Throughfall and litterfall (20% defoliation)	410	0.116	0.118	0.092

All data are per kilogram of foliage. Defoliator data are derived from regressions provided in text.

used to calculate production suggest that herbivore effects should have been detectable.

Foliage nutrient concentrations and nutrient pools were not related to either phytophage. N concentration was 1.1% (±0.35) in new foliage and 0.95% (±0.18) in old foliage, K concentration was 0.69% (±0.15) in new and 0.40% (±0.09) in old foliage, and Ca concentration was 0.19% (±0.06) in new and 0.41% (±0.10) in old foliage. N and K concentrations were similar to values reported for old-growth Douglas-fir, but Ca concentrations were about half (Sollins et al., 1980). These data were used to calculate foliage nutrient pools for evaluation of herbivore effects (Table 1).

Nutrient turnover

Concentrations of N, K and Ca in throughfall were similar to values reported by Sollins et al. (1980). Nutrient concentrations in needle litterfall were 0.95% N (±0.23), 0.17% K (±0.05), and 0.56% Ca (±0.04), within ranges reported by Sollins et al. (1980) and Kiilsgaard et al. (1987). Trends in nutrient content from new foliage to old foliage and litter are similar in direction and magnitude to those reported by Sollins et al. (1980).

Nutrient turnover from the foliage pool was influenced by defoliator abundance during the biologically active early growing season (April–June) (Figs. 2–4). The natural log transformation improved the normality and constancy of variance, and significance and linearity of regression for all variables except throughfall N. The log transformation for throughfall N improved constancy of variance, but resulted in a non-normal distribution of the data and a non-significant regression equation ($P=0.09$; $R^2=0.10$). Litterfall mass (Y_L), throughfall mass (Y_T), throughfall N (Y_N), throughfall K (Y_K), and throughfall Ca (Y_C) were related to average defoliator abundance (X) for this period as follows:

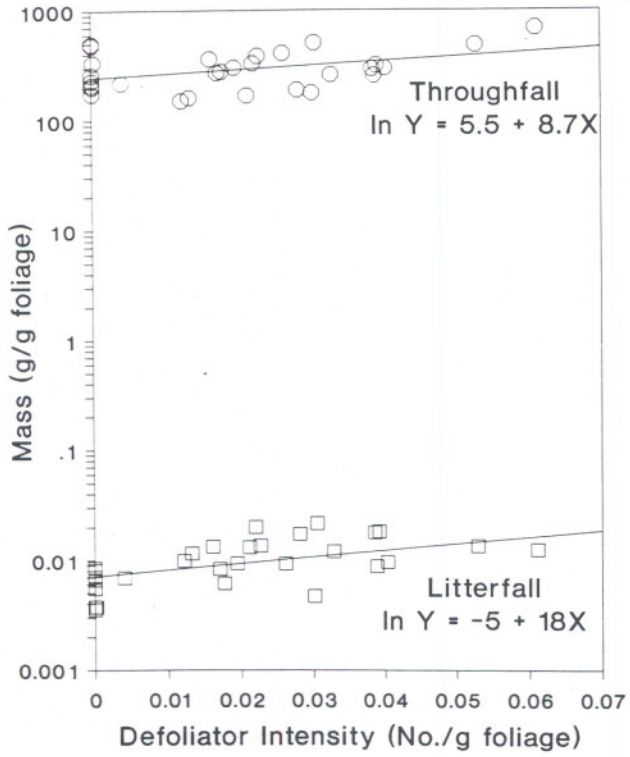

Fig. 2. Defoliator effects on throughfall and litterfall from young Douglas-fir during the early growing season (April–June) at the H.J. Andrews Experimental Forest in western Oregon. Significant least-squares regressions are discussed in text.

$\ln Y_L = -5.0 + 18X$ ($F=16$, df$=1,27$, $P=0.0005$, $R^2=0.37$; Fig. 2)

$\ln Y_T = 5.5 + 8.7X$ ($F=4.6$, df$=1,27$, $P=0.04$, $R^2=0.14$; Fig. 2)

$Y_N = 0.0001 + 0.44X$ ($F=8.4$, df$=1,27$, $P=0.007$, $R^2=0.21$; Fig. 3)

$\ln Y_K = -4.1 + 16X$ ($F=13$, df$=1,27$, $P=0.002$, $R^2=0.30$; Fig. 4)

$\ln Y_C = -5.3 + 24X$ ($F=22$, df$=1,27$, $P=0.0001$, $R^2=0.43$; Fig. 4)

for litter mass and throughfall mass (in g g^{-1} foliage), throughfall N, K and Ca (in mg g^{-1} foliage), and phytophage abundance (in insects g^{-1} foliage). Nutrients in litterfall mass were not related to defoliator abundance, suggesting that nutrients in feces, carcasses, and foliage fragments were leached rapidly from this material and incorporated into throughfall.

Litter mass and throughfall Ca (natural logs) remained significantly related to defoliator abundance during the latter half of the growing season (July–September) ($F=4.3, 5.6$, df$=1,27$, $P=0.048$ and 0.025, respectively). The relationship for throughfall K approached significance at $P=0.078$

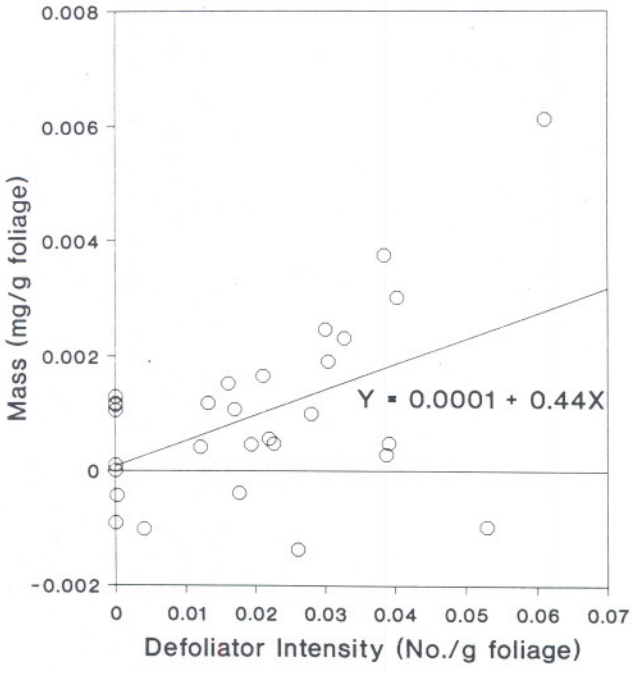

Fig. 3. Defoliator effects on throughfall N from young Douglas-fir during the early growing season (April–June) at the H.J. Andrews Experimental Forest in western Oregon. The significant least-squares regression is discussed in text.

($F=3.3$, df$=1,27$). Only throughfall Ca was significantly related to defoliator abundance for the entire growing season (April–September):

$$\ln Y_C = -5.1+46X \ (F=7.1, \text{df}=1,27, P=0.01, R^2=0.21)$$

for Y_C and X as above, although the relationship for throughfall mass (natural log) approached significance at $P=0.088$ ($F=3.1$, df$=1,27$). Intercepts and slope coefficients for other regressions were similar throughout the growing season. Defoliator effects were not significant for 12–36 month periods.

Nutrient losses from foliage were not related significantly to sap-sucker abundance during April–June or July–September ($P>0.10$). Throughfall K was related to sap-sucker abundance for the growing season (April–September) as follows:

$$\ln Y_K = -3.6+0.72X \ (F=4.8, \text{df}=1,25, P=0.04, R^2=0.16)$$

for Y_K and X as above (Fig. 5). Sap-sucker effects were not significant for 12–36 month periods.

The greater significance of defoliator effects compared with sap-suckers could have resulted from differences in mass intensities. K turnover for equivalent mass intensities (e.g. 10 *A. cooleyi* or 0.01 *L. argentata* weigh

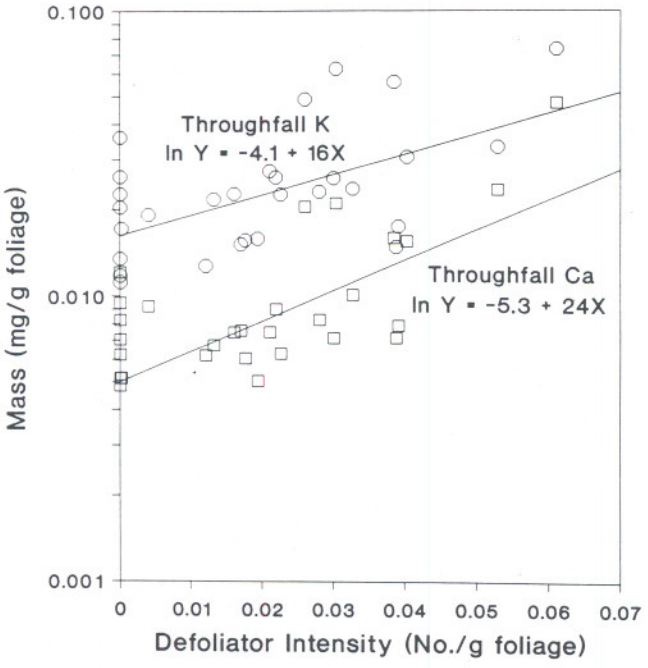

Fig. 4. Defoliator effects on throughfall K and Ca from young Douglas-fir during the early growing season (April–June) at the H.J. Andrews Experimental Forest in western Oregon. Significant least-squares regressions are discussed in text.

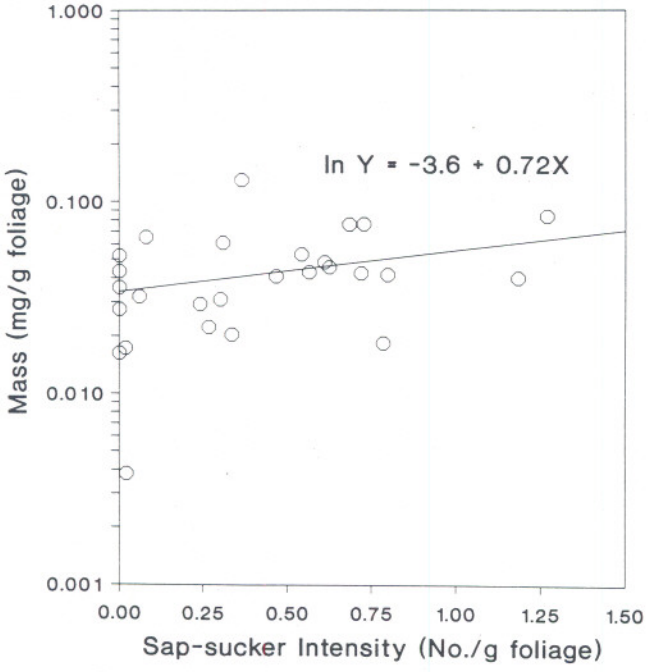

Fig. 5. Sap-sucker effects on throughfall K during the growing season (April–September) at the H.J. Andrews Experimental Forest in western Oregon. The significant least-squares regression is discussed in text.

0.7 mg) for the growing season is three orders of magnitude greater for the sap-sucker than for the defoliator.

Phytophage contribution to nutrient cycling can be calculated from foliage nutrient pools and litter inputs for April–June (Table 1). Defoliators at our highest abundance nearly doubled litterfall and throughfall mass. Defoliator contribution to N, K and Ca turnover at 20% foliage removal was 15–25% of total inputs to litter (Table 1).

Litter decomposition

The exogenous litter used for the litter decomposition study averaged 0.75% ($\pm$0.03) N, 0.48% ($\pm$0.03) K, and 1.24% ($\pm$0.05) Ca, similar to concentrations reported by Sollins et al. (1980) and Kiilsgaard et al. (1987). Concentration of N was somewhat lower than that in litterfall from the experimental trees, but concentrations of K and Ca were about twice the concentrations in litterfall, as presented above.

Litter mass and nutrient content in litterbags at 3, 9, 15, 21, and 27 months generally were not related to phytophage abundances. Litter mass after 3 months and litter N after 15 months (June each year) were related significantly ($F>8$, df=1,27, $P<0.01$, $R^2=0.23$) to sap-sucker abundance, suggesting that this phytophage influenced biological activity early in the growing season. Overall litter decomposition was described by the equation

$$\ln Y = 4.56 - 0.14X \quad (F=880,\ \mathrm{df}=1,270,\ P<0.0001,\ R^2=0.77)$$

where Y is percentage litter mass remaining and X is time in years (Fig. 6).

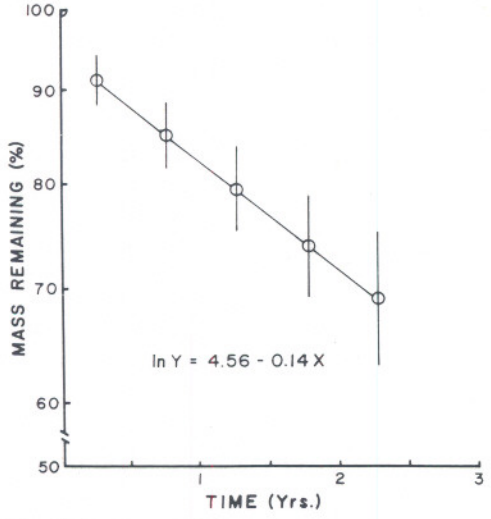

Fig. 6. Decomposition of senescent Douglas-fir needle litter in litterbags for 2.5 years at the H.J. Andrews Experimental Forest in western Oregon. Vertical bars represent 1 S.D. The significant least-squares regression is discussed in text.

The decay rate constant (0.14 $year^{-1}$) is lower than the range 0.21–0.31 reported by Fogel and Cromack (1977) for green needles in mature forests in the western Cascades and indicates a half-time (to 50% loss of mass) of 4.5 years.

Model validation

We compared predicted and observed turnover rates for the 10 unmanipulated trees using our significant regressions above. Our model for phytophage effects on litterfall significantly explained ($F=10$, df=1,8, $P=0.01$, $R^2=0.56$) the variation in litterfall mass for April–June. The utility of models for other turnover processes was constrained by the high variation caused by other environmental factors, particularly precipitation and tree size, as indicated by stepwise multiple regression.

DISCUSSION

We demonstrated that nutrient turnover from foliage to litter was related to phytophage abundance causing up to 20% foliage removal. Although herbivores apparently did not affect calculated tree growth or exogenous litter decomposition, these results are not conclusive.

Our data indicated that phytophage effects on nutrient turnover were important only during the feeding period, and effects can be obscured during seasons of heavy precipitation. Phytophage influences are probably greater at higher defoliation levels and lower precipitation levels. These results support earlier results for an eastern deciduous forest (Schowalter et al., 1981; Seastedt et al., 1983), but indicate a greater effect of phytophages on Ca flow at the Andrews Forest.

Our results for primary production corroborate the 1 year results reported by Seastedt et al. (1983), but neither study killed study trees for direct measurement. Both studies indicate that, for these low levels and short periods of herbivory, trees apparently compensated for losses of foliage and nutrients. Long-term compensatory growth after defoliation has been reported by Wickman (1980) and Alfaro and MacDonald (1988). The doubling in size of our trees within 2 years suggests that resources were sufficient for compensatory growth. Phytophages might have a greater short-term effect on plant growth and nutrient dynamics if nutrients were limiting or herbivory more intense (Schowalter et al., 1986).

Lack of evidence for herbivore effects on exogenous litter decomposition also supports earlier work by Seastedt et al. (1983). The two studies suggest that any herbivore effects on decomposition would be due to differences in litter quality rather than to priming of decomposition by throughfall or litter enhancement. However, Seastedt and Crossley (1983) reported that simu-

lated throughfall (as increased by phytophages in our study) increased comminution of hardwood litter by microarthropods. In our study, adelgid abundance appeared to influence some aspects of decomposition. We also found that two oribatid mites and a pauropod were significantly ($P<0.03$) more abundant in litterbags under defoliated trees (Schowalter and Sabin, 1991). Other factors affecting litter environment, such as degree of moss or herb ground-cover, could have confounded treatment effects, or herbivore effects might become apparent only after a longer period of decomposition.

A key provision of this experiment was the inclusion of a set of monitored but unmanipulated trees for testing our models. Although models developed from manipulated trees were useful only for litterfall, we believe that further work will refine our ability to predict nutrient turnover from data on phytophage functional group composition and abundance, as well as other factors.

In conclusion, our study supports earlier work indicating that low-to-moderate levels of herbivory by forest insects have significant effects on nutrient cycling, primarily through influences on throughfall leaching and litterfall. Expensive efforts often have been expended to suppress these 'pests' in forest ecosystems. Accumulating evidence that phytophages affect nutrient cycling warrants greater effort to clarify the potential contributions of herbivory to productivity and resource values in these ecosystems.

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