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EFFECTS OF CANOPY HERBIVORY ON NUTRIENT CYCLING IN A NORTHERN HARDWOOD FOREST IN WESTERN NORTH CAROLINA

BARBARA C. REYNOLDS,* MARK D. HUNTER, AND D.A. CROSSLEY, JR.

Institute of Ecology, University of Georgia, Athens, GA 30602 USA.
E-mail: kreynolds@unca.edu

ABSTRACT. In May 1998 an outbreak of sawflies, *Periclista* sp. (Hymenoptera: Symphyta), occurred in a high-elevation hardwood forest in western North Carolina. Estimated defoliation of northern red oak (*Quercus rubra*) and white oak (*Q. alba*) removed 40% of leaf area. Weights of frass (insect feces) collected at the site were greater than at a nearby site of lower elevation that was not defoliated. Within a month of the outbreak, elevated levels of nitrate-nitrogen (NO_3-N) were measured in throughfall and resin bag samples from the site and in stream water draining the affected watershed. The lower elevation control watershed did not show increased levels of nitrate-nitrogen in throughfall, resin bags, or stream chemistry. This study demonstrates that insect defoliators can influence ecosystem-level processes such as nutrient cycling.

Key words: canopy, herbivory, nutrient cycling, nitrate, sawflies

INTRODUCTION

As canopy arthropods consume leaves, they take a significant role in regulating nutrient cycling, which is a key process within the forest ecosystem. Input from canopy defoliators to the forest floor includes frass (insect feces), leaf fragments, and modified throughfall (rain that has passed through the canopy). Chew (1974) and Mattson and Addy (1975) were among the first to point out the potential of canopy arthropods to act as key regulators of ecosystem processes.

The role of these insects in forest nutrient cycling has been difficult to demonstrate, because natural outbreaks of canopy herbivores are hard to predict. Background data are, therefore, difficult to obtain. Several researchers, however, have demonstrated the influence of canopy arthropods. Schowalter et al. (1991) used experimental manipulations; Webb et al. (1995) and Eshleman et al. (1998) monitored the effects of gypsy moth outbreaks; and Swank et al. (1981) used long-term data on ecosystem properties that include a period of natural insect outbreak.

Swank et al. (1981) demonstrated "functional, ecosystem-level consequences of feeding activities of forest defoliators," in their study of the fall cankerworm (Lepidoptera: Geometridae). This moth, *Alsophila pometaria* Harris, is a native spring defoliator of hardwood forests from southern Canada to north Georgia. An outbreak of the fall cankerworm was first observed in 1969 on the Coweeta basin in western North Carolina; it continued until 1978. The center of the outbreak was Watershed 27 (WS27), a 38.8 ha control catchment with undisturbed mixed hardwoods at an elevation of 1001–1347 m above sea level. Mean monthly concentrations of nitrate-nitrogen (NO_3-N) in the stream that drains WS27 were elevated compared to stream NO_3-N from an undisturbed catchment, WS18. Winter concentrations usually were highest, although elevated concentrations also were apparent in late April through early June, during and after the feeding period of the fall cankerworm. By 1978 the cankerworm population had returned to background levels, and NO_3-N concentrations also declined.

In May 1998, an outbreak of sawflies (Hymenoptera: Symphyta) occurred in the same area as the fall cankerworm outbreak—along the highest parts of WS27 (1347 m) and up the ridges to the highest points on the Coweeta basin (1609 m). Sawflies were observed feeding on red oak, *Quercus rubra* L., and white oak, *Q. alba* L. The defoliation lasted approximately 2–3 weeks, peaking at the end of May. A study conducted by the authors in 1998 found evidence that the sawfly outbreak contributed to increases in NO_3-N export from WS27. The study compares nutrient concentrations during the sawfly outbreak in spring with those reported for the fall cankerworm outbreak.

Sawflies are a phytophagous suborder of the Hymenoptera. The unidentified species observed at Coweeta is in the genus *Periclista,* which is associated almost exclusively with oaks. The adults emerge early in the spring and lay their eggs on leaves (Smith 1969). Larvae typically emerge 1–2 weeks later and undergo 5–6 instars. Mature larvae generally pupate in the soil (Smith 1993). There is one generation per year. The May 1998 outbreak was unusual, because *Periclista* normally occur at low population lev-

* Corresponding author

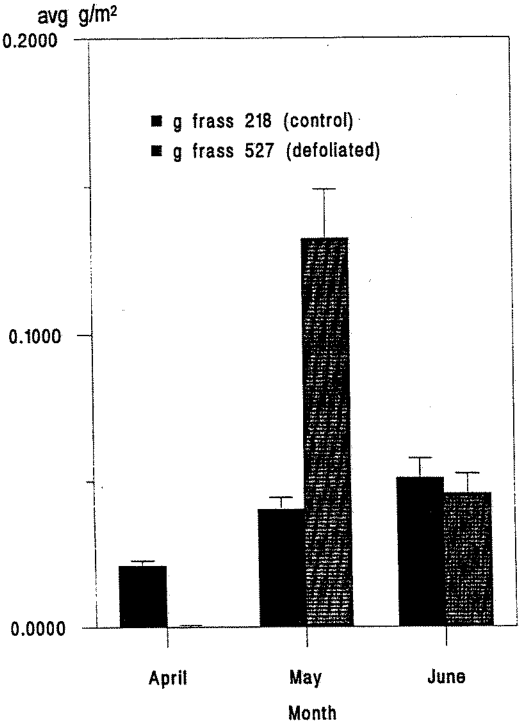

FIGURE 1. Frass inputs (avg. g/m²) on study sites 218 (control) and 527 (defoliated) at Coweeta, North Carolina, 1998.

els and rarely cause extensive damage (D.R. Smith pers. comm.).

MATERIALS AND METHODS

Research was conducted at the Coweeta Hydrologic Laboratory of the United States Forest Service, which is located in the Nantahala Mountain Range of western North Carolina within the Blue Ridge Physiographic Province, 35°03′N and 83°25′W. Established in 1934, Coweeta has elevation ranges of 675–1592 m. With more than 60 years of research data on its watersheds, Coweeta has one of the longest continuous environmental records available (Swank & Vose 1997).

As part of an ongoing study of canopy herbivory and its effects on forest floor processes, collectors were established in 1996 to sample frass, throughfall, and soil water (Reynolds & Crossley 1997). Two of the sites with collectors in that study were 527 and 218. Site 527 is the high-elevation (1347 m) northern hardwood forest with a northeast-facing slope on WS27 where the sawfly outbreak occurred. Common tree species on this site include red oak; red maple, *Acer rubrum* L.; striped maple, *A. pensylvanicum* L.; and yellow birch, *Betula lutea* Michaux. Chestnut oak, *Q. prinus* L., and white oak are common in areas adjacent to the site. Site 218 is a lower elevation site (795 m) on WS18, on a north-facing slope. The undisturbed cove terrain contains hardwoods such as tulip poplar, *Liriodendron tulipifera* L.; red maple; red oak; sweet birch, *B. lenta* L.; and hickory, *Carya* sp. No outbreak of sawflies or other phytophagous insects was observed on site 218 in 1998. Chestnut oak is common in the surrounding forest.

Throughfall (precipitation that falls through the canopy) was collected in 26.0 cm diameter funnels connected by plastic tubing to 5-gallon plastic buckets. The funnels had plastic screen circles, 75 mm in diameter, with openings of 2.0 × 3.0 mm in their throats. Although the main purpose of the screens was to keep leaves and other detritus out of the throughfall, the mesh size was small enough to exclude most frass. Most sawfly frass, however, had fallen before the throughfall collectors were set up. Throughfall, collected weekly when precipitation exceeded 0.1 inch, was combined on a monthly basis. Throughfall collections were made June–September to check for any lingering effects of defoliation. Frass was collected during 24-hour dry periods in small laundry baskets lined with plastic bags. Typically frass collections were made twice monthly. Throughfall and frass collectors were placed in 20 randomly selected plots at each site. Ion exchange resin bags, both anion and cation (Binkley 1984, Binkley et al. 1986), were placed in the A horizon of the soil, approximately 2–3 cm below the humus layer on 10 of the 20 plots. Each bag contained one tablespoon of resin. Bags were left in the soil for two months, after which their contents were extracted one time in 1 molar potassium chloride for 2 hours. Resin extracts and throughfall were analyzed for NO_3-N on an Alpkem Flow-Injection Analyzer. Stream grab samples from gauged catchments were collected weekly and are part of a record beginning in 1972 (Swank & Crossley 1988). Stream NO_3-N was analyzed using EPA Method 300.0, "Inorganic anions in water by ion chromatography," on a Dionex 4500i Model II.

Visual herbivory estimates for site 527 were made in late May and again in late July following the outbreak. At that time, herbivory estimates also were made along Ball Creek Road below and above site 527. Multiple observers cross-checked the estimates using seven damage classes (Hunter 1987, Hunter & Schultz 1995).

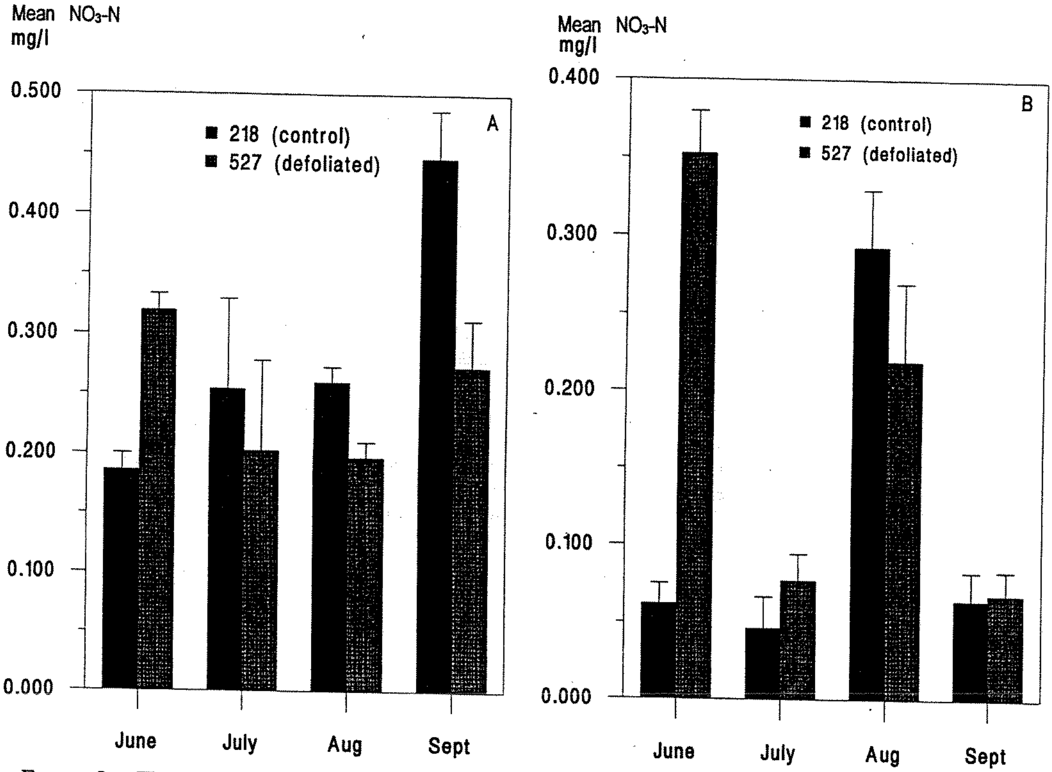

FIGURE 2. Throughfall inputs (avg. mg/l NO_3-N) on study sites 218 (control) and 527 (defoliated). A = 1997, B = 1998.

RESULTS AND DISCUSSION

Leaf area removed (LAR) was 10–20% at the bottom of WS27 at an elevation of 1001 m. Observed herbivory increased with elevation. At the top of WS27, at an elevation of 1347 m, 40% LAR was noted on study site 527. Continuing up the ridge to the highest points of the Coweeta basin, at an elevation of more than 1500 m, we observed 60–70% LAR.

The probable influence of the sawfly outbreak can be traced beginning with frass inputs in May 1998 (FIGURE 1). In April, site 527 had few leaves and little measurable frass; but by May, frass inputs on site 527 tripled that on site 218 (control). Because no other insect herbivores were abundant on site 527 during this time, most of the frass collected presumably came from the sawflies. Average frass inputs from June were not significantly different between sites.

NO_3-N concentrations in June 1998 throughfall were much higher on site 527 compared to the low-elevation control. This same pattern, however, was observed in 1997 when there was no outbreak (FIGURE 2). Previous investigations at Coweeta (B.L. Haines et al. unpubl.) found elevated concentrations of NO_3-N in throughfall during and after the maximum cankerworm defoliation; but we can not attribute the high NO_3-N in the 1998 throughfall from site 527 exclusively to the effects of sawfly herbivory. Insect frass and greenfall (green leaves and leaf portions that fall as a result of insect feeding) also are potential sources of NO_3-N input.

Concentrations of NO_3-N in resin extracts, representing soil solution chemistry, were five times greater for the June/July sampling on site 527 than on site 218. Resin NO_3-N was also much higher for site 527 in June/July compared to samples from both sites taken for April/May and August/September (FIGURE 3). Because the resin samples were taken during a 2-month period, resolution is insufficient to determine when the increase in NO_3-N on site 527 occurred. With tree species composition and aspect similar at the two sites, we attribute the increase to the influence of sawfly herbivory. Although Coweeta experienced its second driest growing season on record in 1998, rainfall in June was normal and similar for high and low elevations. July precipitation was about one-sixth the normal

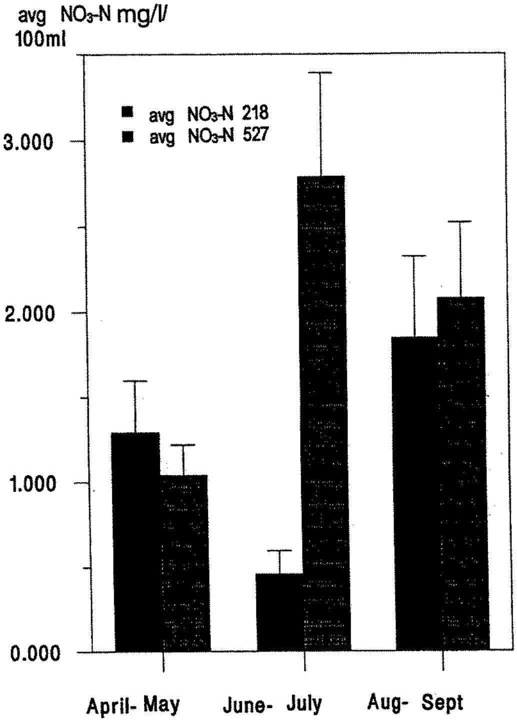

FIGURE 3. Resin concentrations (avg. NO_3-N mg/l/ 100 ml 1 M KCl extract) from study sites 218 (control) and 527 (defoliated), 1998.

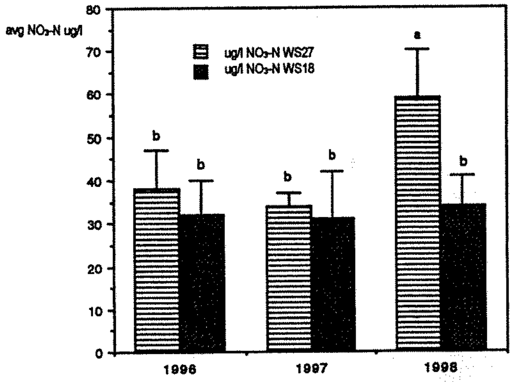

FIGURE 4. Average concentrations of NO_3-N for a defoliated WS27 stream and control WS18, with values derived from analyses of weekly grab samples and concentrations weighted by measured flow volumes, June–August, 1998. Bars with same letter within groups are not statistically different.

amount for both elevations, although the higher elevation had twice as much rain as the lower elevation (L. Swift pers. comm.). It is reasonable, then, to assume that any influences from precipitation on NO_3-N in the resin bags occurred in June, when the greatest ion movement caused by moisture in the soil would have occurred.

Mean NO_3-N concentrations in the WS27 stream were elevated for the period June–August 1998 compared to the previous two years (FIGURE 4). During the same months in 1998, NO_3-N concentrations in WS27 were significantly higher than those in the WS18 stream. These concentrations were weighted by measured flow volumes, which would take into account any difference in flow caused by decreased precipitation in 1998. Swank et al. (1981) reported the greatest NO_3-N export during the high flow of winter months following defoliation, caused by greater concentrations of NO_3-N and higher streamflow during winter and spring. The winter of 1997–1998 presumably had even higher concentrations of NO_3-N leaving WS27. Webb et al. (1995) also reported increased stream NO_3-N following forest defoliation, in that case by the gypsy moth, *Lymantria dispar*.

Although the effects found in our study are similar to those reported by Swank et al. (1981), the magnitude of NO_3-N export in 1998 was greater than that reported for the fall cankerworm outbreak. Mean monthly NO_3-N concentrations for the WS27 stream in 1998 were 67–80 ug/l. In contrast, the highest reported concentrations during the cankerworm outbreak were less than 60 ug/l. Mean monthly NO_3-N concentrations in the control stream draining WS18 generally were also higher in 1998 than during the cankerworm outbreak. These higher nitrogen values are attributed to increased nitrogen deposition at Coweeta, as measured by a 25-year bulk precipitation record. Control watersheds at Coweeta are thus in a transition phase between state 0 and state 1 of N saturation (Aber et al. 1989, Swank & Vose 1997) or between state 1 and 2 (Aber et al. 1998). Another cause of the higher nitrogen values is decreased biological demand by maturing forest stands (Swank & Vose 1997).

CONCLUSION

Evidence suggests that a short-term, one-season defoliation event caused a conspicuous increase in NO_3-N levels in soil and in the stream draining the affected watershed; and the defoliation had an ecosystem-level effect on nutrient cycling. As Swank and Vose (1997) point out, even low-level responses of NO_3-N indicate substantial changes in the internal N-cycle, because baseline systems tend to be highly conservative of nitrogen. Our study demonstrates the value of long-term data sets in providing background data for comparison when a natural perturbation occurs.

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