Insect Defoliation Enhances Nitrate Export from Forest Ecosystems

W.T. Swank, J.B. Waide, D.A. Crossley, Jr., and R.L. Todd

1 Coweeta Hydrologic Laboratory, Otto, North Carolina 28763
2 Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37830
3 Department of Entomology, University of Georgia, Athens, Georgia 30602
4 Department of Agronomy, University of Georgia, Athens, Georgia 30602, USA

Summary. Chronic defoliation by the fall cankerworm, Alsophila pomataria (Harris), accompanied substantial increases in the stream export of nitrate nitrogen (NO$_3$-N) from three mixed hardwood forests in the southern Appalachians. These integrated results clearly demonstrate a measurable effect of insect consumers on ecosystem processes, and provide support for the regulatory importance of insects on a landscape scale.

Introduction

Phytophagous insects have recently been postulated to act as regulators of forest primary production and nutrient cycling (Matison and Addy 1975, Kitchell et al. 1979). However, there is little direct evidence available at the ecosystem level to determine the impacts of grazing insects on total system processes. An interdisciplinary research program on forest biogeochemistry at the Coweeta Hydrologic Laboratory provides a unique opportunity to examine the effects of a defoliator on forest processes. In this paper, we describe the integrated effects as reflected in stream chemistry.

The fall cankerworm (Lepidoptera: Geometridae) is a native spring defoliator of hardwood forests from southern Canada to northern Georgia and northwest to Missouri, Montana, and Manitoba. Isolated populations have been reported from Colorado and California (Porter and Alden 1924). An epidemic or outbreak population of this geometrid in Macon County, North Carolina, was first observed adjacent to and on the Coweeta Basin in western North Carolina in 1969 (Flavell and Lambert 1970). Watershed 27 (WS-27), a 38.8-ha control catchment with a cover of undisturbed mixed hardwoods, was the primary site of infestation. Defoliation progressed from the higher elevations (1,400 m) on the catchment in 1970 toward lower elevations in ensuing years.

Results and Discussion

Baseline measurements of stream chemistry were initiated on 22 gaged catchments located throughout the Coweeta Basin beginning in 1972 (Swank and Douglass 1975). The stream draining WS-27 showed atypically high levels of NO$_3$-N compared to other undisturbed control catchments (Fig. 1). Mean monthly concentrations of NO$_3$-N in streams draining undisturbed hardwood forests at Coweeta are generally below 10 μg l$^{-1}$; however, levels on WS-27 frequently rose above 30 μg l$^{-1}$. Highest concentrations typically occurred during winter, with large spikes also generally seen during and immediately following the time period of cankerworm feeding (late April through early June). In 1974, when cankerworm populations appeared to peak, and approximately 33% of the total leaf mass was consumed (Waide et al. unpublished data), concentrations were elevated throughout the year. In subsequent years, infestation (as measured by estimated levels of defoliation) was less severe and in 1978, the population returned to endemic or nonoutbreak levels, due in part to egg parasitism by the microhymenopteran, Telenomus alsophilae Vier. (U.S. Department of Agriculture 1979, Pettigrew 1980). This decline in the cankerworm population was accompanied by a return of NO$_3$-N concentrations toward baseline levels in 1979 (Fig. 1).

Accelerated stream export of NO$_3$-N concomitant with defoliation was also detected on WS-36, another high elevation catchment (48.5 ha) located in the Coweeta Basin, about 2 km from WS-27. In contrast to WS-27, cankerworm infestation was not present on the catchment when stream chemistry analyses were initiated. Thus, during the period from 1972 through 1973, mean monthly NO$_3$-N concentrations were representative of other undisturbed forest ecosystems at Coweeta; i.e., generally below 10 μg l$^{-1}$ (Fig. 1). Concentrations began rising in late spring 1974 in response to the outbreak of defoliating populations of cankerworms. Egg-mass surveys on trees in 1975 confirmed that infestation had occurred over significant portions of the catchment. In ensuing years, defoliation was not as severe as on WS-27, and NO$_3$-N levels on WS-36 were lower. By 1979, concentrations had returned to baseline levels (Fig. 1).

No changes in concentrations of other nutrients such as ammonia-nitrogen, phosphorus, sulfate, and major cations were detected in the streams draining these two catchments, partly because baseline values are usually higher and differences in bedrock mineralogy between nondefoliated and defoliated control catchments influence some inorganic ions sufficiently to mask small changes in ionic composition.

The impact of full cankerworm defoliation on NO$_3$-N export was also observed during the conduct of a separate study in the Nantahala Mountains of western North Carolina, about 13 km northwest of the Coweeta Basin. This study was designed to assess the effects of logging on stream chemistry and involved sampling of four streams, including one stream draining a control forest and three streams draining hardwood forests scheduled for clearcutting. In the 16-month pretreatment calibration period of February 1973 to May 1974, NO$_3$-N concentrations averaged 8 μg l$^{-1}$ in the three streams draining catchments scheduled for cutting. Concentrations were higher and more variable in the control stream, particularly during the early summer months, and averaged 20 μg l$^{-1}$ for the calibration period. In the first
Fig. 1. Mean monthly concentrations of NO$_3$-N in streams draining control and partially defoliated, hardwood-covered catchments at Coweeta Hydrologic Laboratory. Monthly values are derived from analyses of weekly grab samples; concentrations are weighted by measured flow volumes. Nitrate-nitrogen was determined colorimetrically on an autoanalyzer using sulfanilamide and a cadmium reduction column.

Fig. 2. Seasonal increased export of NO$_3$-N in streamflow from WS-27, Coweeta Hydrologic Laboratory. Winter (W) = December–February; Spring (SP) = March–May; Summer (S) = June–August; and Fall (F) = September–November. The change in export of NO$_3$-N was estimated by multiplying WS-27 flow volumes by monthly concentration differences between defoliated and control catchments (WS-27 – WS-18).

Table 1. Average annual weighted stream concentration and annual output of NO$_3$-N on WS-27, WS-36, and on WS-18, an undisturbed control catchment, Coweeta Hydrologic Laboratory

<table>
<thead>
<tr>
<th>Calendar Year</th>
<th>WS-27 Conc. (µg/l)</th>
<th>WS-27 Output (g/ha)</th>
<th>WS-36 Conc. (µg/l)</th>
<th>WS-36 Output (g/ha)</th>
<th>Undisturbed control WS-18 Conc. (µg/l)</th>
<th>Undisturbed control WS-18 Output (g/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972</td>
<td>16</td>
<td>240</td>
<td>6</td>
<td>105</td>
<td>2</td>
<td>105</td>
</tr>
<tr>
<td>1973</td>
<td>16</td>
<td>310</td>
<td>4</td>
<td>86</td>
<td>3</td>
<td>86</td>
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<tr>
<td>1974</td>
<td>25</td>
<td>456</td>
<td>15</td>
<td>219</td>
<td>6</td>
<td>219</td>
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<tr>
<td>1975</td>
<td>20</td>
<td>284</td>
<td>8</td>
<td>152</td>
<td>4</td>
<td>152</td>
</tr>
<tr>
<td>1976</td>
<td>16</td>
<td>276</td>
<td>4</td>
<td>85</td>
<td>3</td>
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<tr>
<td>1977</td>
<td>15</td>
<td>243</td>
<td>6</td>
<td>108</td>
<td>2</td>
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<tr>
<td>1978</td>
<td>19</td>
<td>213</td>
<td>6</td>
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<td>1979</td>
<td>12</td>
<td>253</td>
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<td>77</td>
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</tbody>
</table>

Year following forest cutting (June 1974–June 1975), average NO$_3$-N concentrations in the three treated streams increased to 20 µg l$^{-1}$, and in the second year to 28 µg l$^{-1}$. These results were not unexpected based on data from previous cutting experiments at Coweeta (Swank and Douglass 1977). However, annual NO$_3$-N concentrations in the control stream increased to 49 and 77 µg l$^{-1}$ in the second and third years of the study. These high levels of NO$_3$-N in the “control” stream were again associated with extensive cankerworm defoliation in the headwater areas of this catchment. Infestations appeared to be even more severe than at Coweeta.

The effects of defoliation on annual weighted concentrations and the total export of NO$_3$-N from the hardwood forest ecosystems on WS-27 and WS-36 as contrasted with an undisturbed control (WS-18) are shown in Table 1. Annual weighted concentrations on WS-27 are typically fourfold to fivefold greater compared to those on the undisturbed control catchment. Excluding the years of documented infestation on WS-36 (1974 and 1975), annual concentrations of NO$_3$-N in this stream averaged 5 µg l$^{-1}$, a value close to that observed on the lower elevation, undisturbed control. In terms of annual NO$_3$-N export, it appears from WS-36 data that baseline values for high elevation watersheds at Coweeta lie between 75 and 100 g ha$^{-1}$ yr$^{-1}$. Thus, during peak insect activity on WS-27 in the years between 1973 and 1975, NO$_3$-N loss was increased about 250 g ha$^{-1}$ yr$^{-1}$ with a general decline in succeeding years. Annual export from WS-36 was smaller but obviously increased during peak infestation years followed by a decline in later years.
Seasonal analyses of NO$_3$-N discharge consistently show that more than 80% of the increased export occurred during the winter and spring months between December and May (Fig. 2). This was due to the combined factors of elevated concentrations and higher streamflow during these seasons compared to the remainder of the year. Elevated concentrations were also typically seen in June and July (Fig. 1), but low streamflow amounts during these months produced only slightly increased exports of NO$_3$-N.

Previously it has been reported that defoliation by the saddled prominent, Heterocampa guttivita (Walker), did not lead to measurable increases in the stream export of NO$_3$-N or other nutrients from aggrading forest ecosystems at the Hubbard Brook Experimental Forest, New Hampshire (Bormann and Likens 1979). In contrast to Coweeta, baseline concentrations of NO$_3$-N in streams draining control forests at Hubbard Brook are high (> 1,000 µg l$^{-1}$). The magnitude of change in NO$_3$-N concentrations reported here for Coweeta is considerably smaller than the standard error of the mean NO$_3$-N concentrations at Hubbard Brook (Likens et al. 1977), and hence not statistically detectable at that site. Moreover, the duration of defoliation at Hubbard Brook was apparently shorter than at Coweeta.

Results presented above clearly demonstrate increased stream export of NO$_3$-N during periods of intense cankerworm defoliation of southern Appalachian hardwood forests. This insect grazing has measurably altered biogeochemical processes at the ecosystem level of organization. The watershed responses reported here represent the integrated functional properties of an entire forest ecosystem, and are the results of coupled biogeochemical processes operating within forest ecosystems.

During the period of cankerworm defoliation, we also conducted research at the process level in an attempt to explain why defoliation leads to increased NO$_3$-N export. This research will be reported in detail elsewhere, but the following changes took place in defoliated forests: (i) wood production decreased but leaf production increased, leading to apparent increases in total aboveground net primary production; (ii) large inputs of frass and contained elements to the forest floor; (iii) large increases in leaf litterfall; (iv) measurable increases in total litter-soil metabolism (CO$_2$ efflux) and standing crops of both total microbes (ATP content) and nitrifying bacteria (MPN counts), which were synchronized with the timing of larval cankerworm feeding; and (v) significant increases in pools of available elements (especially mineral N) in upper soil horizons. Taken together, these results suggest a temporary shift from wood to leaf production, increased rates of nutrient uptake, increased litter turnover rates, and especially an acceleration of rates of recycling and turnover of (labile) elements in litter-soil horizons. Collectively these responses should stimulate future levels of primary production on sites where defoliation was concentrated, a hypothesis to be tested in subsequent research. If confirmed, then cankerworm defoliation may indeed be viewed as a major factor regulating the biogeochemistry of forest ecosystems in the Appalachian Mountains of the eastern United States.

These results represent one of the clearest demonstrations yet reported of functional, ecosystem-level consequences of the feeding activities of forest defoliators. The significance of the increased loss of NO$_3$-N lies in the alteration of nutrient transfer and turnover rates associated with forest defoliation, and the consequences of such functional changes for the persistence and metabolism of the forest ecosystem over long time periods. Only via an improved understanding of such ecosystem dynamics at broad space-time scales of resolution can appropriate management strategies for forest insect populations be devised and implemented. Mechanisms and longer-term dynamics of cankerworm defoliation remain under active study by our group.

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