Contribution of Herbivore-caused Greenfall to Litterfall Nitrogen Flux in Several Southern Appalachian Forested Watersheds

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ABSTRACT.—Herbivorous insects are responsible for a portion of foliar litterfall in forest ecosystems. There is little information on the nutrient content of this litterfall despite speculation that herbivores regulate nutrient cycles. We quantified herbivore-caused “greenfall” (green leaves falling as a direct result of herbivore feeding activity) in four Appalachian watersheds and analyzed samples for total nitrogen. Concentrations of nitrogen in greenfall fluctuated significantly from May through September and were always higher than concentrations of nitrogen in autumn senesced leaves. Annual inputs of greenfall nitrogen ranged from 0.08–0.18 g m⁻² yr⁻¹ and resulted in 3.2% to 6.5% of total nitrogen transferred to the forest floor in autumn foliar litterfall. Greenfall is viewed as a high-quality substrate supplying nitrogen to decomposer organisms and is thus a potential mechanism by which herbivorous insects speed nutrient cycling.

INTRODUCTION

Insect herbivores may regulate productivity in terrestrial ecosystems (Mattson and Addy, 1975) and nutrient cycling (Kitchell et al., 1979; Schowalter, 1981; Seastedt and Crossley, 1984) even under typical conditions of chronic, nominal herbivory. Surprisingly little information exists, however, to support or refute a herbivore role in eastern deciduous forests. For example, herbivore-caused litterfall and its nutrient content have been measured and related to nutrient cycling in few studies (see Gosz et al., 1972; Kimmins, 1972; Larrson and Tenow, 1980; Ohmart et al., 1983; Hollinger, 1986). Although most related studies have limited their scope to insect fecal pellets (e.g., Gosz et al., 1972), the activities of leaf-eating insects also contribute to foliar litterfall.

We quantified herbivore-caused foliar litterfall (“greenfall”) in four forested southern Appalachian watersheds where greenfall occurred from spring leaf flush to autumn leaf senescence (Risley and Crossley, 1988). Greenfall was caused by several species of insects and was represented by all trees, shrubs and vines (approximately 35 species) in the study area. Because herbivorous insect feeding activities responsible for greenfall (e.g., caterpillars that partially consume a leaf blade, then sever the petiole) cause petiole injury sufficient to detach leaves, they are likely to restrict or prevent translocation of nutrient elements from these leaves. Thus, greenfall should, in general, be nutrient-rich. This suggestion was based upon indirect evidence and related work by Larrson and Tenow (1980). We hypothesized that if greenfall is rich in nutrients, particularly nitrogen, then greenfall could serve as a high-quality substrate (relative to other surface litter) available for rapid use by decomposer organisms, thus speeding nutrient cycling (Risley and Crossley, 1988). Nitrogen was emphasized because it is considered a limiting nutrient in many terrestrial ecosystems (Swift et al., 1979), and may “regulate the productivity of forests” (Waide et al., 1988). Nitrogen is not easily leached from attached leaves and is readily translocated from senescing leaves...
into plant storage organs (Gosz et al., 1975); therefore, herbivory resulting in rapid detachment of damaged leaves may be an important mechanism by which nitrogen is released from the canopy during the growing season. Because nitrogen is readily translocated from senescing leaves, nitrogen content of damaged leaves cannot, however, be inferred as identical to nitrogen content of undamaged live foliage.

In this study, herbivore-mediated transfers of nitrogen in greenfall from the tree canopy to the forest floor were examined with two goals; the first was to interpret greenfall as a resource for decomposer organisms and the second was to contribute to knowledge of the function of herbivores in forest nutrient cycles.

**Materials and Methods**

Research was conducted within the forested 1626 ha Coweeta basin at the Coweeta Hydrologic Laboratory, U.S. Forest Service, Otto, North Carolina (35°N, 83°25'W). The Coweeta basin ranges in elevation from 675 to 1592 m and the terrain is rugged with slopes averaging 50 to 60% (Swank and Crossley, 1988). Plant communities, typical of the southern Appalachians, are species-rich and dominated by deciduous oaks (Day et al., 1988).

Greenfall and other litterfall were collected from four watersheds which were selected based on long-term records of herbivory by insects, topographic similarities, and differences in stand age. At the time of the study, watershed 7 (WS7, S-facing) was in the 8th yr of regeneration following a commercial clear-cut and cable-logging. Watershed 13 (WS13, E-facing) was in the 23rd yr of regeneration following two clear-cuts (1939, 1962) where no products were removed. Watersheds 2 (WS2, S-facing) and 18 (WS18, N-facing) have been undisturbed since 1923 and serve as references with which to compare effects of watershed treatments.

Ten 5 × 5 m plots were established randomly along logging roads that bisected each watershed. Plots were located several meters beyond obvious soil disturbance and roadside vegetation boundaries. Greenfall leaves and leaf fragments were collected off the forest floor in each plot every 2 wk, from 13 May through 20 September 1985. Some leaf fragments (<1 cm$^2$) may not have been detected on the forest floor. Based on herbivore damage to leaf petioles, greenfall was categorized initially as either "herbivore-caused" or "unexplained." Unexplained greenfall was excluded from greenfall biomass calculations and from nitrogen analyses. Portions of greenfall samples categorized as herbivore-caused were dried to constant weight at 50 C, weighed, ground, digested in sulfuric acid with hydrogen peroxide and a selenium catalyst, and analyzed colorimetrically (total Kjeldahl nitrogen—TKN) using a Technicon AutoAnalyzer® (Reynolds and Deal, 1988). Graphs describing greenfall nitrogen inputs to the forest floor were constructed using mid-April and mid-October as the beginning and end, respectively, of seasonal greenfall. Areas under the curves were calculated using the trapezoidal method of integration to estimate total annual inputs of greenfall nitrogen.

Litter traps with interior measurements of 62 × 66 cm (0.41 m$^2$), with wood sides and aluminum window screen bottoms, were mounted level approximately 40 cm above the forest floor. One trap was placed 1–2 m from the side (furthest from the road) of each greenfall plot. From these traps foliar and other litterfall (e.g., twigs, fecal pellets) were collected monthly from June 1985 through February 1986. In the laboratory, litter samples were separated into components (e.g., plant species, insect fecal pellets, twigs, etc.) and dried to constant weight at 50 C. Estimates of the nitrogen content of woody and "miscellaneous" litterfall were derived from Monk and Day (1988). In a separate, unrelated study autumn foliar litterfall was collected from randomly placed litter traps, separated by species, and analyzed for nitrogen as described for greenfall (B. C. Reynolds, pers. comm.). We used these data to estimate nitrogen concentrations in trap-collected foliar litterfall.
Paired t-tests were used to compare concentrations of greenfall nitrogen between collection dates within each watershed (alpha = 0.05, n = 10) (Zar, 1984). Watershed comparisons were limited to concentrations of greenfall nitrogen between disturbed and reference watersheds (n = 2). Additional statistical comparisons between watersheds were not made because they provide limited inference and may imply inappropriate tests of watershed treatment effects (Hurlbert, 1984).

RESULTS AND DISCUSSION

Concentrations of total Kjeldahl nitrogen (TKN) in greenfall were between 1.5% and 3.25%, and are generally comparable to concentrations in foliage collected by Day and Monk [1977; see their Fig. 2 (mislabeled twigs)] from dominant tree species at Coweeta during the growing season (Fig. 1). The paper by Day and Monk (1977) is one of the few to address intraseasonal changes in concentrations of foliar elements; and, because their study took place at Coweeta, it serves as the best source for comparison with our data. No herbivore outbreaks or any other major disturbances were documented during their study.

Total Kjeldahl nitrogen in greenfall in each watershed was, for all collection dates, significantly higher (P < 0.05) than TKN in autumn foliar litterfall (Fig. 1). The concentrations of nitrogen in greenfall, therefore, support our suggestion that herbivore activity resulting in greenfall prevents or slows translocation of nitrogen from these damaged leaves.

There were relatively large contributions of nitrogen-rich successional species to greenfall: primarily black locust (Robinia pseudoacacia) and grapes (Vitis spp.) on WS7, and yellow poplar (Liriodendron tulipifera) on WS13 (Risley and Crossley, 1988). Because nitrogen concentrations in foliage of these “early successional” species is significantly higher compared to other woody species at Coweeta (Boring et al., 1988), we expected differences between disturbed and reference watersheds. However, statistical comparisons were not significant (P > 0.05) for any collection date.

Intraseasonal variability in greenfall nitrogen was pronounced (Fig. 1) and followed a similar pattern on each watershed. This variability departed from data presented by Day and Monk (1977) that described slowly decreasing concentrations of foliar nitrogen during the growing season. Highest concentrations of greenfall TKN were measured from samples collected 13 May and 7 July. From 13 May to 5 June and from 7 July to 21 July there were significant decreases (P < 0.05) in greenfall TKN in each watershed. Initial peaks (13 May) in greenfall TKN corresponded to spring leaf flush. Explanation of the second peak in greenfall TKN is uncertain. It is likely due, in part, to secondary leaf production where young, expanding leaves are high in nitrogen whether they flush in spring or later in the season (Mattson, 1980). Similar secondary leaf production was included in Day and Monk’s data (1977) and a corresponding secondary peak in foliar nitrogen is not apparent in their figures. Because caterpillars are highly selective in choosing leaves to consume (Schultz, 1983) and may switch from plant parts low in nitrogen to those higher in nitrogen (McNeill and Southwood, 1978; Mattson, 1980), greenfall-causing insects, primarily caterpillars, may have preferentially selected these young, nitrogen-rich leaves. Greenfall in mid- to late summer was composed of relatively small young leaves compared with larger “mature” leaves of the same species (pers. observ.).

Combining information contained in Figure 1 with data on greenfall biomass (Risley and Crossley, 1988) yielded inputs of greenfall nitrogen to the forest floor (Fig. 2). Intraseasonal patterns of nitrogen inputs exhibited considerable variation that reflected intraseasonal changes in the suite of insect species responsible for greenfall and their relative abundances. This dynamic was, in turn, responsible for the variable contributions of 25 species of trees and woody vines. In general, inputs of greenfall biomass to the forest floor
Fig. 1.—Concentrations of nitrogen (% TKN) (means ± 95% CI; n = 10) in greenfall (May–Sept.) and in autumn foliar litterfall (Oct.) in four southern Appalachian watersheds. WS2 = S-facing, disturbed since 1923; WS7 = S-facing, 8 yr regeneration following clear-cut; WS13 = E-facing, 8 yr regeneration following clear-cut; WS18 = N-facing, undisturbed since 1923.

Nitrogen concentrations were light but steady during the growing season but were magnified by relatively high concentrations of nitrogen especially early in the season.

Integration of greenfall nitrogen inputs using graphs constructed from Figure 2 yielded estimates of the total seasonal flux of greenfall nitrogen (Table 1). Inputs of greenfall...
Fig. 2.—Inputs of greenfall nitrogen (mg/m²) (means ± 95% CI; n = 10) from the canopy to the forest floor in four southern Appalachian watersheds.

Nitrogen were highest in WS2 (undisturbed, S-facing). This was not unexpected because long-term studies of herbivory in the forest canopy at Coweeta have shown that rates of herbivory are typically higher in WS2, relative to other low-elevation watersheds (Crossley et al., 1988).
### Table 1

Annual inputs of foliar nitrogen (means ± SE; n = 10) to the forest floor in four southern Appalachian watersheds. Annual inputs of greenfall nitrogen were derived by integrating areas under curves (Fig. 1). Annual inputs of nitrogen in autumn foliar litterfall were based upon litter biomass from this study and nitrogen content of litterfall (Reynolds, pers. comm.).

<table>
<thead>
<tr>
<th>Nitrogen Flux</th>
<th>WS2</th>
<th>WS7</th>
<th>WS13</th>
<th>WS18</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greenfall (g/m²/yr)</td>
<td>0.17</td>
<td>0.09</td>
<td>0.10</td>
<td>0.10</td>
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<tr>
<td>(0.031)</td>
<td></td>
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<tr>
<td>Autumn foliar litterfall (g/m²/yr)</td>
<td>2.72</td>
<td>2.76</td>
<td>3.08</td>
<td>2.96</td>
</tr>
<tr>
<td>(0.097)</td>
<td></td>
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<tr>
<td>Proportional contribution of greenfall N (%)</td>
<td>6.52</td>
<td>3.30</td>
<td>3.43</td>
<td>3.56</td>
</tr>
<tr>
<td>(1.178)</td>
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</tbody>
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Nitrogen flux in autumn foliar litterfall was similar among watersheds despite differences in aspect, treatment history and plant species dominance (Table 1). For example, nitrogen inputs in autumn foliar litterfall were similar in the clear-cut WS7 and adjacent, undisturbed WS2 despite differences in production of nitrogen-rich Robinia pseudoacacia foliage on WS7 (34.7 g/m² in WS7 and 0.7 g/m² in WS2). Nitrogen inputs contributed by autumn foliar litterfall represented 80–90% of nitrogen flux in total litterfall [total litterfall foliar + woody + “miscellaneous” litterfall; nitrogen content of woody and miscellaneous litter derived from Day and Monk (1977)].

Because nitrogen inputs to the forest floor in autumn foliar litterfall were similar among watersheds, the pattern of relative contributions of greenfall nitrogen to nitrogen inputs by autumn foliar litterfall were also similar to annual inputs of greenfall nitrogen to the forest floor (Table 1). Greenfall in WS2 (undisturbed, S-facing) contributed the highest percentage (approximately 6.5%) of nitrogen to the forest floor compared to the other watersheds (3–7%). Again, this may reflect greater herbivore intensity in WS2, thus higher inputs of greenfall biomass that included nitrogen-rich plant species. Although seasonal inputs of greenfall nitrogen to the forest floor were relatively small, the occurrence of greenfall throughout the entire growing season and its high nitrogen content make it a predictable and high-quality substrate for decomposer organisms. We view greenfall as a potential mechanism by which herbivorous insects speed nutrient cycling.

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**References**


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