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Effects of endemic densities of canopy herbivores on nutrient dynamics along a gradient in elevation in the southern Appalachians

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Summary

In southern Appalachian forests, outbreaks of insect herbivores have been shown repeatedly to increase the availability of nutrients in soil and the export of nitrate in forest streams. The mechanisms underlying herbivore-induced changes in nutrient dynamics include inputs of insect frass (feces) and modification of precipitation as it passes through the forest canopy (throughfall). Here, we consider the effects of endemic (non-outbreak) populations of insect herbivores on soil processes in the southern Appalachians. We measured inputs of frass and throughfall at three elevations at the Coweeta Hydrologic Laboratory, North Carolina. We also measured soil nutrient availability and soil respiration. Inputs of total frass, frass nitrogen and frass carbon exhibited early- and late-season peaks, with those peaks occurring earlier at low elevation where leaf flush begins first. The C:N ratio of frass generally increased over time at all elevations, presumably reflecting seasonal declines in foliar nitrogen. Nitrate in throughfall generally increased over time, whereas throughfall phosphate declined and throughfall ammonium remained relatively constant. Relationships among frass deposition and throughfall nutrients varied with elevation. At low elevation, frass nitrogen was strongly correlated with throughfall nitrate, but this relationship was absent at mid and high elevation. The relationships between frass deposition and throughfall ammonium were inconsistent among elevations. The availabilities of nitrate and ammonium in soil were both related to frass deposition. For example, frass deposition in May explained about 62 % of the variance in soil nitrate availability. Soil respiration exhibited summer maxima at all elevations and was related primarily to soil temperature. There was also a weak positive relationship between the C:N ratio of frass and soil respiration. Overall, we suggest that endemic densities of canopy herbivores can influence forest soil processes, but that the relationships exhibit pronounced spatial and temporal variability.

Key words: Canopy herbivores, defoliation, forest ecosystems, frass, insect populations, nitrogen dynamics, nutrient availability, soil processes, soil respiration

Key phrases: Herbivore inputs and soil processes, defoliation and nutrient dynamics, linking canopy and forest floor processes, herbivore effects on nutrient cycling

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Introduction

During the 1960s and 1970s, it was suggested that herbivores could regulate nutrient cycling and primary production in ecosystems (Pitelka 1964; Schultz 1964 1969; Chew 1974; Mattson and Addy 1975; Kitchell et al. 1979). Subsequently, some studies indicated that moderate levels of herbivory could increase rates of nutrient cycling (Schowalter 1981; Seastedt and Crossley 1984; DeAngelis 1992) and stimulate productivity. However, it has become increasingly clear that the effects of herbivores on nutrient cycling are complex and depend upon a suite of factors including the type of herbivore, the level of herbivory, and the ecological community under investigation (Hunter 2001). The literature provides clear examples of both positive effects (Swank et al. 1981; Seastedt and Crossley 1984; DeAngelis 1992; Belovsky and Slade 2000; Reynolds et al. 2000) and negative effects (Hatton and Smart 1984; Pastor et al. 1993; Pastor et al. 1998; Ritchie et al. 1998; Knops et al. 2000) of herbivory on rates of nutrient cycling. This variation in ecosystem response to herbivore activity has been the focus of our recent work with insect herbivores in forest systems.

There are seven broad mechanisms by which the activity of insect herbivores can cause changes in nutrient cycles and nutrient availability in soils (Hunter 2001). These are (i) deposition of frass (feces), (ii) inputs of insect cadavers, (iii) defoliator-mediated changes in the chemistry of precipitation (throughfall), (iv) changes in the quality and quantity of litter inputs, (v) changes in nutrient uptake by the plant community, (vi) effects upon root exudation and root/mutualist interactions, and (vii) effects upon the physical structure of plant canopies and the subsequent changes in soil microclimate. Examples of each are provided in Hunter (2001) and here we focus upon the effects of insect frass on nutrient dynamics in a temperate forest ecosystem.

Insect herbivores can deposit significant quantities of fecal material (frass) onto litter and soil. Nitrogen returned to soils in insect frass can exceed that in leaf litter (Fogal and Slansky 1985; Grace 1986), and can double overall rates of nitrogen return from plants to soil (Hollinger 1986). More importantly, in temperate systems, frass inputs occur at a different time of year from natural litter fall and include resources that would, in the absence of herbivory, be resorbed by perennial plants before leaf drop. For example, about 70 % of foliar nitrogen is resorbed by oaks prior to senescence under low levels of herbivory. Under heavy defoliation, however, resorption can be reduced to less than 25 % of foliar nitrogen, with 29 % lost in premature leaf fall, 23 % in insect frass, and 8 % in insect biomass (Lovett et al. 2002). Under isolated California oak trees, up to

70 % of both the nitrogen and phosphorus that returns to the soil is in the form of frass and cadavers during outbreaks of the California oak moth (Hollinger 1986). Although a considerable proportion of forest canopies can be turned over annually by insect herbivores (Lowman 1992), inputs are obviously much smaller in the absence of outbreaks. Under endemic insect densities (less than 10 % foliage removed), herbivores are thought to consume around 2–3 % of annual leaf production in *Eucalyptus* forest and return less than 4 % of nitrogen, phosphorus, and potassium to the forest floor as frass (Ohmart et al. 1983).

At our study site in the southern Appalachians, insect outbreaks can result in marked changes in nutrient cycling and export of nitrate in forest streams. For example, defoliation by the fall cankerworm is followed by an increase in primary productivity, increases in litterfall, increases in nutrient inputs to the soil in frass and throughfall, increases in soil nitrogen pools and increases in soil microflora (Swank et al. 1981; Swank and Crossley 1988). Likewise, infestations of black locust by the locust stem borer in the same forests coincide with nitrate export in forest streams (Crossley et al. 1988). Recently, a moderate outbreak (40 % leaf area removed) of the oak-feeding sawfly *Periclista* sp. (Hymenoptera: Tenthredinidae) led to a tripling of average frass inputs and a five-fold increase in soil nitrate availability. Summer increases in soil nitrate were followed by two-fold increases in stream nitrate export in autumn and winter (Reynolds et al. 2000). Experimental additions of frass to forest floors in the southern Appalachians have resulted in blooms of Collembola, fungal-feeding nematodes, bacterial-feeding nematodes, and predatory mites (Reynolds et al. 2003). Presumably, these soil invertebrates are responding to fungal and bacterial blooms (Coleman and Crossley 1996) resulting from the nutrient additions in frass.

In the present study, we were interested in measuring inputs of nutrients in frass, and their consequences for nutrient dynamics, under endemic densities of insect herbivores in the southern Appalachians. As Lovett et al. (2002) point out, there is a real need for studies that assess links between low levels of defoliation and nutrient dynamics in forests. Specifically, we wished to estimate variation in frass inputs along a gradient in elevation and to associate frass deposition with (i) nutrient deposition in throughfall, (ii) nutrient availability in the soil, and (iii) soil respiration. Our purpose was to determine whether the relationships between nutrient dynamics and herbivore activity observed under insect outbreak (Swank et al. 1981; Crossley et al. 1988; Reynolds et al. 2000, 2003; Reynolds and Hunter 2001) were also observed under endemic densities of insect herbivores.

Materials and Methods

Study sites

Our study was conducted at the Coweeta Hydrologic Laboratory, operated by the US Forest Service. Coweeta is in the Nantahala Mountain Range of western North Carolina, within the Blue Ridge Physiographic Province at latitude 35° 03' N and longitude 83° 25' W (Swank and Crossley 1988). Our three sites within Coweeta have similar aspects and vegetation but range in elevation from 795 m (low) through 1000 m (mid) to 1347 m (high) (Reynolds and Crossley 1995). Classification of soils includes Typic and Humic Hapludults (low elevation), Typic Dystrochrepts (mid elevation) and Typic Haplubrepts (high elevation) (Knoepp and Swank 1998). The differences in elevation among sites translate into differences in the length of the growing season, with tree bud burst beginning two weeks later, and leaf fall beginning two weeks earlier, at high elevation than at low elevation (M. D. Hunter, unpublished data).

Herbivore inputs

We established 20 sampling stations (replicates) within 40 m circles at each elevation. At each sampling station, we estimated inputs of frass (insect feces) from the canopy, and the nutrient concentration of throughfall (precipitation after passage through the canopy). We measured the concentration of nutrients in throughfall because it represents a further pathway by which frass, dissolved in solution, might enter the litter/soil nutrient pool. However, we recognize that herbivore-mediated changes in throughfall nutrients represent the combined effects of nutrient leaching from damaged leaves (Tukey and Morgan 1963) and the dissolution of frass from foliage. Frass was collected in small laundry baskets, lined with plastic bags, that were opened for 24 h dry periods approximately weekly from May through August, 1999 (10 sample dates per site). Frass samples were collected individually (20 replicates per site per date), returned to the laboratory, dried at 60° C for 24 h, and weighed. We estimated %C, %N, and C:N ratio for each sample using a Carlo-Erba C/N analyzer and converted estimates of C and N inputs to the soil to g ha^{-1} 24h^{-1} from the surface area of frass traps.

Throughfall was collected in 26 cm diameter funnels, with 75 mm plastic screen circles to exclude most litter fall, connected by plastic tubing to five-gallon plastic buckets. We collected throughfall weekly from May through August, 1999, so long as the water completely covered the bottom of the bucket. We recorded the volume of water and collected a 23 ml sample from each bucket on each date. For each month, we generated a composite sample for each bucket (replicate) with proportional amounts of throughfall from each collection date. We therefore generated a total of 240 samples; 4 dates (months) by 20 replicates by 3 elevations. Samples were then analyzed for NO_3-N, NH_4-N, and PO_4-P using the automated cadmium reduction, phenate, and automated ascorbic acid reduction methods respectively (Greenberg et al. 1992) on an Alpkem Flow-Injector Analyzer.

Soil nutrients and soil respiration

We estimated the availability of nutrients in the soil at 10 of the 20 sampling stations per site. Pairs of ion exchange resin bags, containing positively and negatively charged resin in knee-high nylon hose (Binkley 1984; Binkley et al. 1986), were inserted in the soil approximately 5 cm deep. Bags were placed by cutting into the soil at an angle to the soil surface, minimizing the disturbance to soil above bags. Each bag was approximately 16 sq cm and contained 10 g of resin. Resin bags were initially installed in early May, 1999, and then replaced with fresh resin bags every month until the end of August, 1999, for a total of four resin bag collections. The contents of the resin bags were extracted in 100 mL of 1 M KCl and analyzed for NO_3-N, NH_4-N, and PO_4-P as for throughfall samples (above).

Soil respiration measurements were made with a PP Systems EGM-2 Environmental Gas Monitor (PP Systems, Haverhill, MA). This instrument uses a non-dispersive infrared measurement technique combined with a soil respiration chamber (Parkinson 1981). A soil temperature probe (STP-1) was coupled to the EGM-2. We made measurements of soil temperature, at a depth of approximately 5 cm, with every respiration measurement. The monitor was calibrated monthly using known concentrations of CO_2 (lab) or atmospheric CO_2 (field). Estimates of soil respiration were made at the same 10 sampling stations per elevation at which resin bags were located. Our intention was to measure soil respiration monthly (May through August, 1999), however equipment failure resulted in no measurements for June. Measurements were made on May 18, July 13, and August 16 and data are reported as g CO_2 m^{-2} hr^{-1}.

Statistical Analyses

In general, the data failed to meet the assumptions of normality. Consequently, all analyses were carried out using generalized linear models (Proc Genmod, SAS Inst. 1996) with poisson distributions and log link func-

tions. Final models were selected by back-stepping procedures from full models to obtain the most parsimonious model with the highest log likelihood ratio (Agresti 1996). We initially analyzed weekly frass inputs to establish seasonal patterns and to assess variation among elevations. In subsequent analyses, frass inputs were averaged by month to facilitate comparison with estimates of throughfall nutrients, soil nutrients, and soil respiration that were gathered monthly. Finally, to estimate the relative contribution of frass to variation in throughfall nutrients, soil nutrients, and soil respiration, we employed parametric analyses of variance components (SAS Inst. 1996). Because the data are not normally distributed, these parametric analyses cannot be used to provide a probability value for accepting or rejecting a particular relationship – those are provided by the Genmod Procedures. Rather, they provide the reader with a rough estimate of the relative importance (or lack thereof) of insect frass to soil processes such as nutrient availability and respiration.

Results

Weekly frass inputs

All sites exhibited both early- and late-season peaks in frass deposition, with the early-season peaks occurring first at low elevation, second at mid elevation, and last at high elevation. (elevation* date interaction $\chi^2 = 26.19$, d.f. = 2, P < 0.0001, Fig. 1). These patterns probably reflect differences in the phenology of leaf-flush which occurs first at low elevation sites. Nitrogen deposition in frass showed somewhat similar patterns (elevation*date interaction $\chi^2 = 31.11$, d.f. = 2, P < 0.0001, Fig. 2), although a pronounced late-season peak was only detected at low elevation. Carbon deposition in frass (Fig. 3) mirrored the patterns observed for the mass of frass (elevation*date interaction $\chi^2 = 22.82$, d.f. = 2, P < 0.0001). The C:N ratios of frass were generally lowest at the beginning of the season and highest towards the end of the season ($\chi^2 = 9.06$, d.f. = 1, P = 0.0026, Fig. 4). Declines in foliar nitrogen concentration (and therefore increases in foliar C:N ratios) are probably responsible for the changes in frass C:N ratio over time. Seasonal declines in foliar nitrogen concentration have been reported for several forest tree species (Feeny 1970; Schultz et al. 1982; Hunter & Schultz 1995).

Monthly throughfall nutrients

Temporal patterns of nutrient concentration in throughfall from the forest canopy were not closely allied with temporal patterns of frass inputs. Throughfall
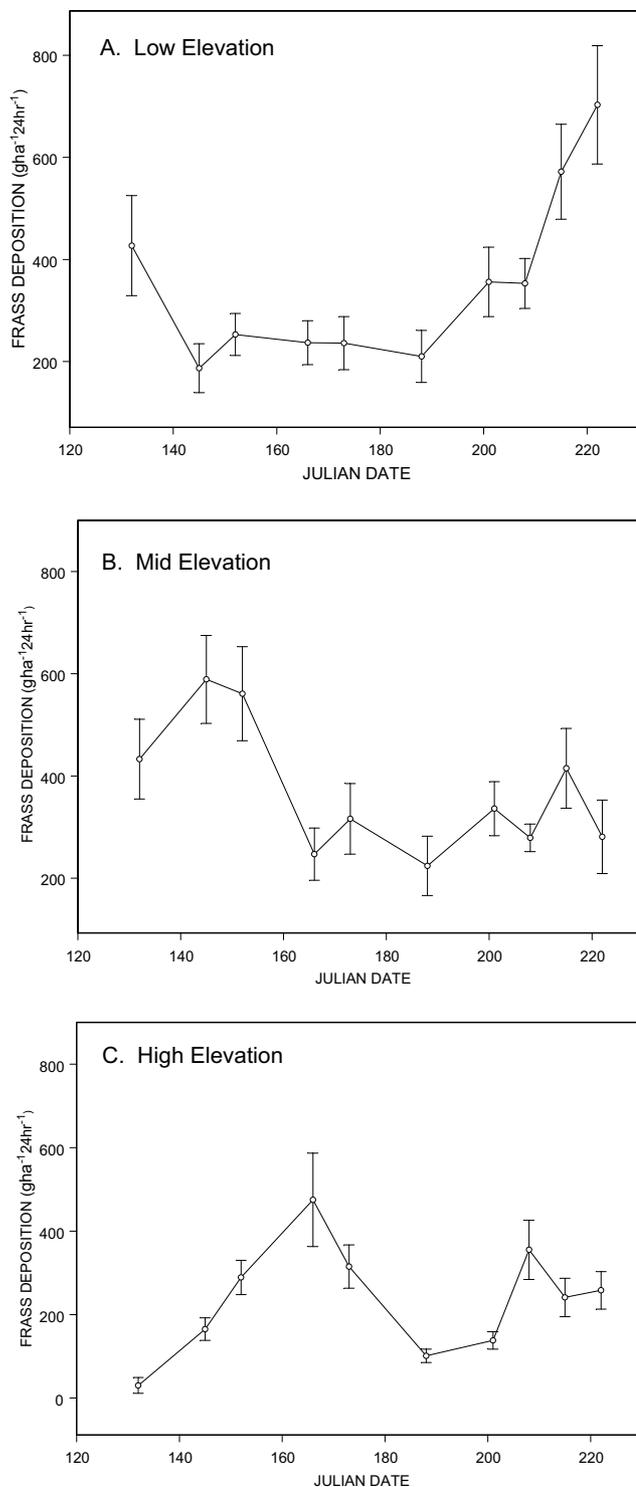

Fig. 1. The deposition of frass (g ha⁻¹ 24 hr⁻¹) at three elevations at the Coweeta LTER Site in North Carolina. Data are the means of 20 samples ± S.E.

Fig. 2. The deposition of nitrogen in frass (g ha^{-1} 24 hr^{-1}) at three elevations at the Coweeta LTER Site in North Carolina. Data are the means of 20 samples ± S.E.
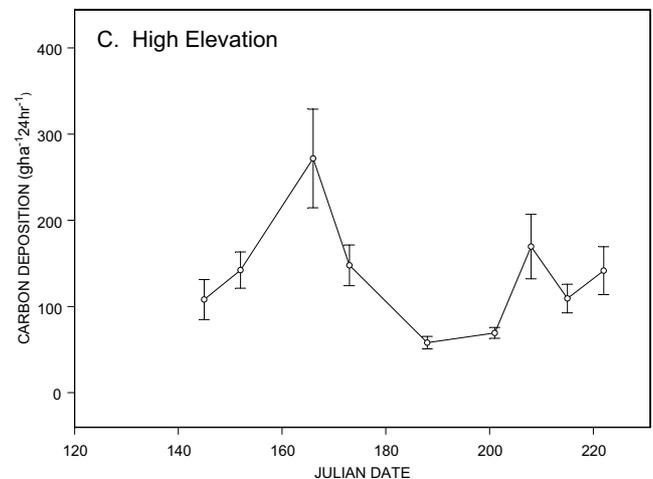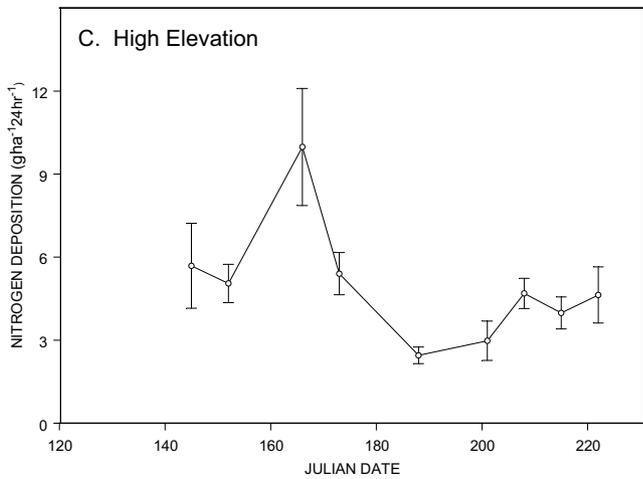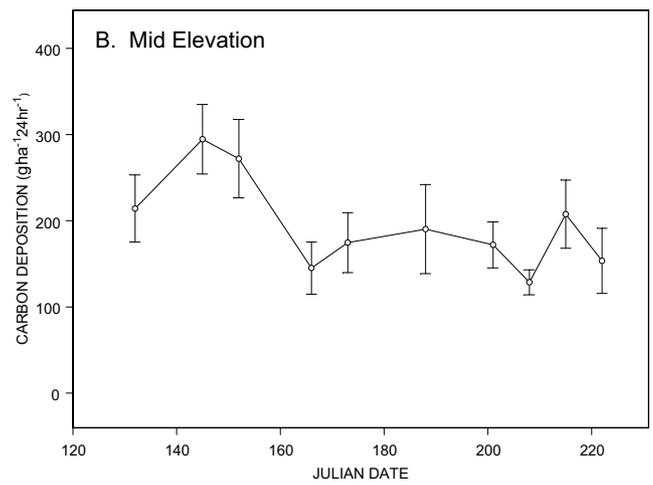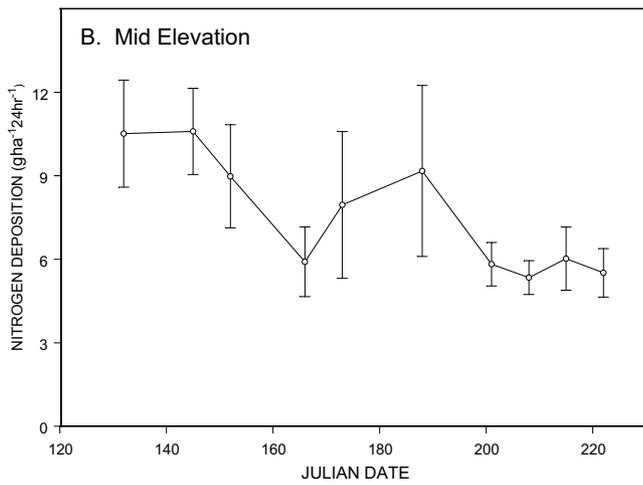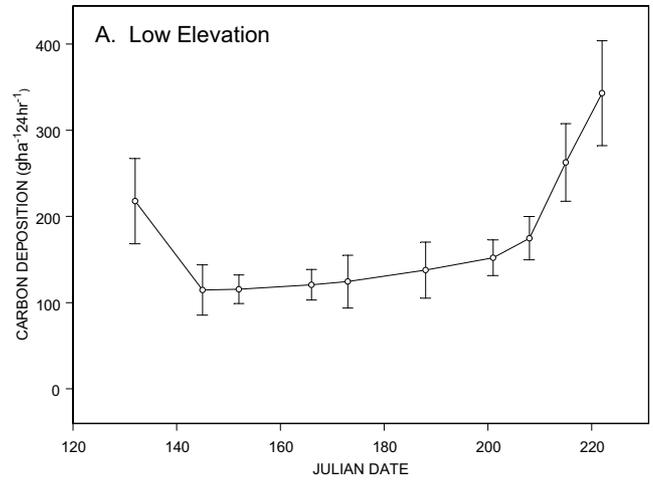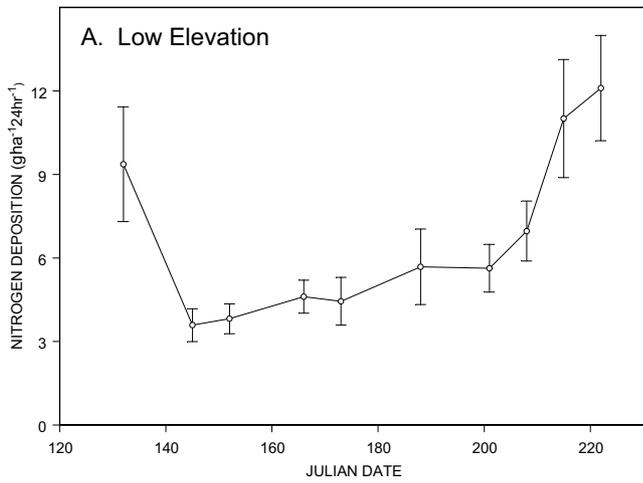
Fig. 3. The deposition of carbon in frass (g ha^{-1} 24 hr^{-1}) at three elevations at the Coweeta LTER Site in North Carolina. Data are the means of 20 samples ± S.E.
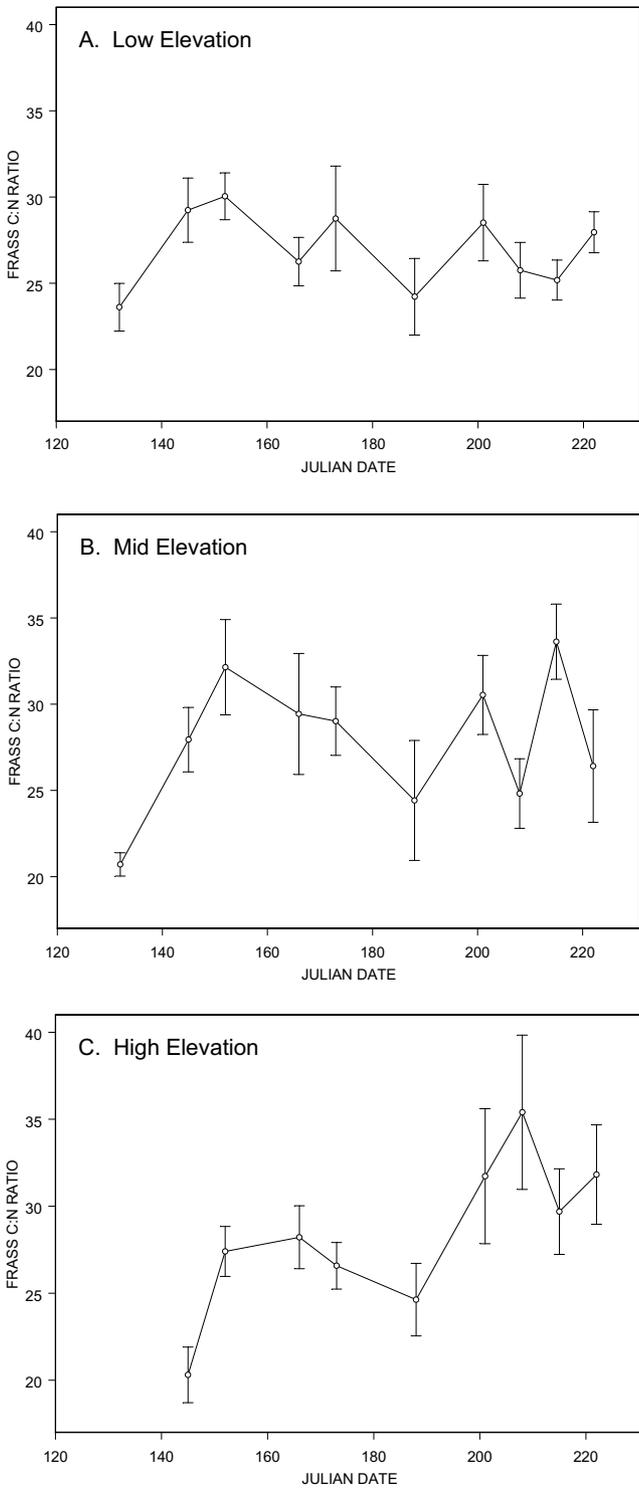
Fig. 4. Seasonal changes in the C:N ratio of frass falling from the canopy to the forest floor at three elevations at the Coweeta LTER Site in North Carolina. Data are the means of 20 samples ± S.E.
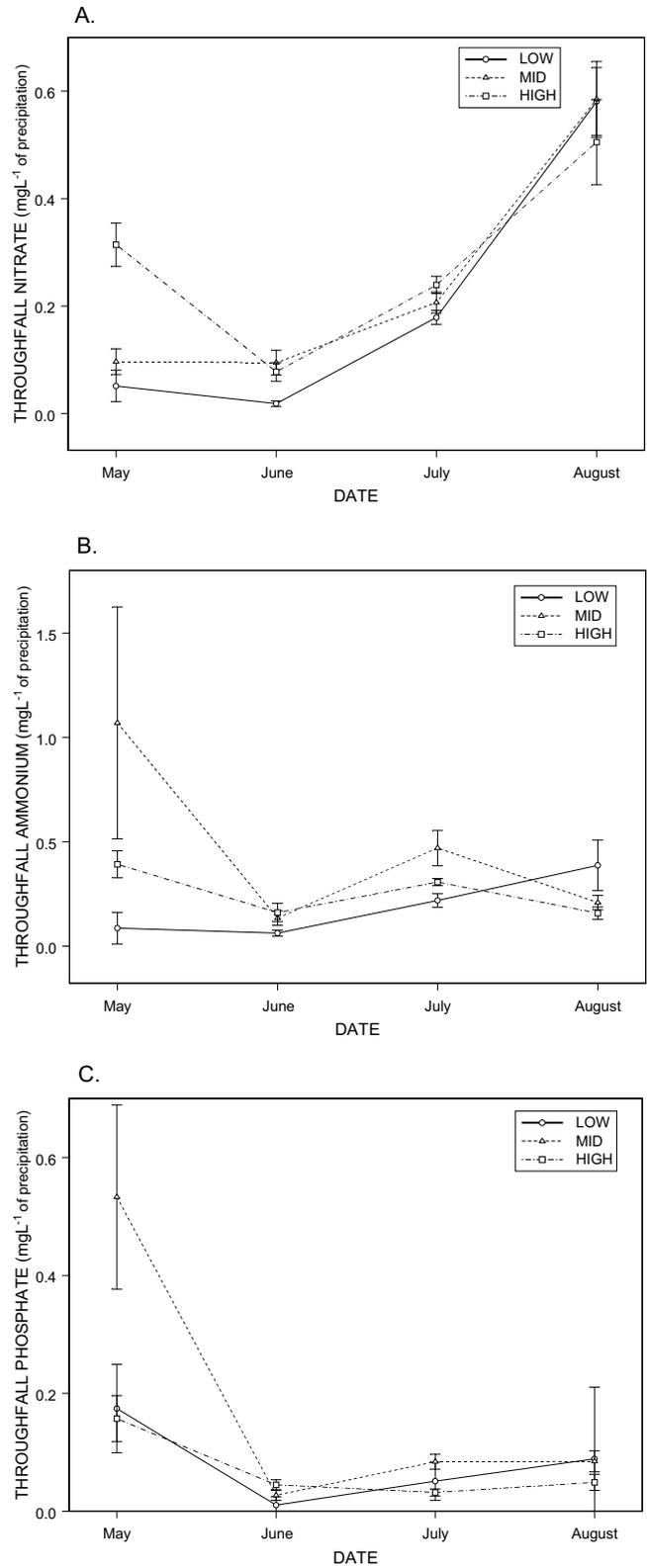

Fig. 5. Seasonal changes in the deposition of A) nitrate, B) ammonium, and C) phosphate in throughfall at three elevations at the Coweeta LTER Site in North Carolina. Data are given as mg L^{-1} of precipitation and represent the means of 20 samples ± S.E.

Fig. 6. Seasonal changes in soil respiration (g CO_2 m^{-2} hr^{-1}) at three elevations at the Coweeta LTER Site in North Carolina. Data are the means of 10 samples ± S.E.
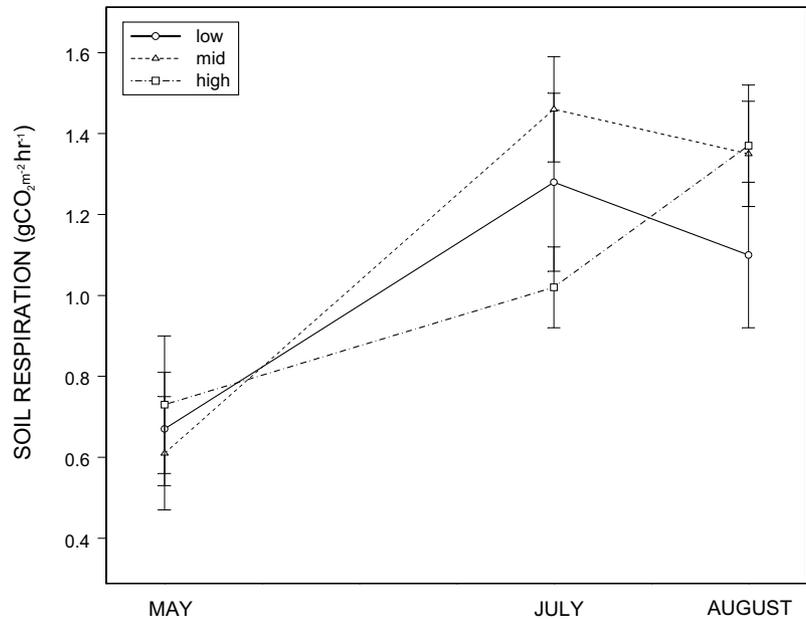
nitrate concentrations increased during the season (Fig. 5A), although initial concentrations were high at high elevation (elevation*date interaction χ^2 = 30.56, d.f. = 2, P < 0.0001). Throughfall ammonium concentrations were generally similar throughout the season (Fig. 5B), except for a pronounced early-season peak at mid elevation (elevation*date interaction χ^2 = 7.95, d.f. = 2, P = 0.0004). Throughfall phosphate concentrations declined at all elevations by early summer (date effect χ^2 = 21.45, d.f. = 1, P < 0.0001, Fig. 5C), although the mid elevation site again showed a more pronounced early-season peak (site effect χ^2 = 13.13, d.f. = 2, P = 0.0014).

Monthly soil respiration

Soil respiration exhibited summer maxima at all elevations (date effect χ^2 = 37.39, d.f. = 1, P < 0.0001, Fig. 6), probably related to high summer soil temperatures (below). There were no significant differences in respiration among elevations, nor an elevation*date interaction.

Relationships between frass and throughfall nutrients

The nitrate concentration of throughfall from the forest canopy increased with the deposition of nitrogen in insect frass, but only at low elevation (elevation*frass nitrogen interaction χ^2 = 17.65, d.f. = 2, P < 0.0001, Fig. 7A). A parametric estimate of variance components suggested that frass nitrogen deposition ex-

plained 27 % of the variance in throughfall nitrate at low elevation, and less than 2 % at mid or high elevation. In contrast, the ammonium concentration of throughfall was positively related to the mass of frass deposited at low elevation, unrelated to frass at mid elevation, and negatively related to frass deposition at high elevation (χ^2 = 14.71, d.f. = 1, P < 0.0001 and χ^2 = 12.93, d.f. = 1, P = 0.0003 at low and high elevation, respectively, Fig. 7B). A parametric estimate of variance components suggested that frass deposition explained 17 % of the variance in throughfall ammonium at low elevation, less than 1 % at mid elevation, and 13 % at high elevation. However, the change in the direction of the relationship between frass deposition and throughfall ammonium between low and high elevation suggests that there may be no simple link between the two. The phosphate concentrations of throughfall were unrelated to any of the measurements (mass, N, C, C:N) taken from frass in this study.

Relationships between frass and soil nutrient availability

Estimates of soil nitrate availability (resin bags) were positively related to frass deposition in May and July, but unrelated to deposition in June or August (frass*date χ^2 = 7.67, d.f. = 1, P = 0.0056, Fig. 8A). The relationship was particularly strong in May (χ^2 = 23.40, d.f. = 1, P < 0.0001) when a parametric estimate of variance components suggested that frass deposition explained 62 % of the variance in soil nitrate availability. Variance explained was 20 % in July
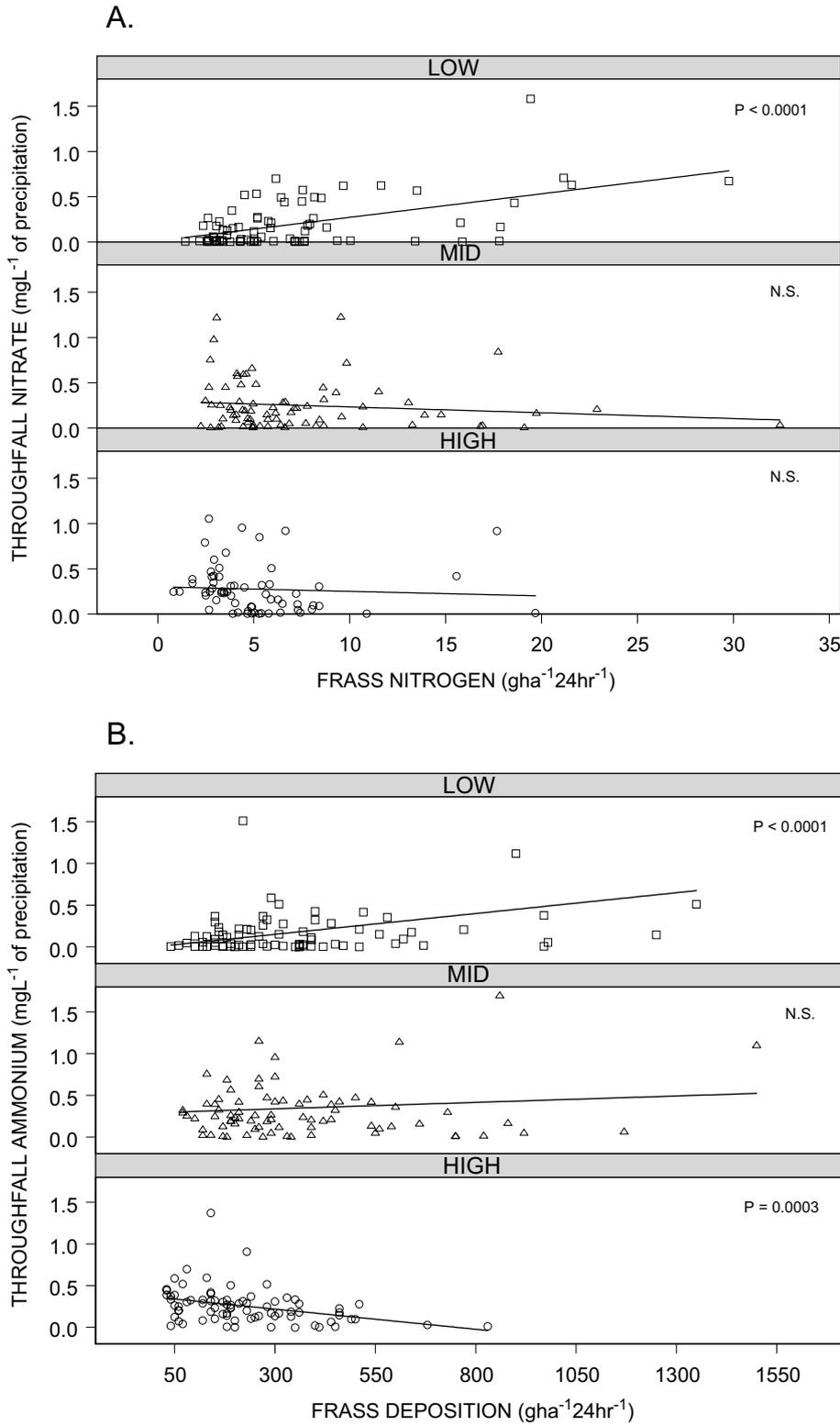
Fig. 7. Relationships between A) nitrate and B) ammonium in throughfall and the deposition of A) frass nitrogen and B) total frass weight at three elevations at the Coweeta LTER Site in North Carolina. N = 80 (20 samples × 4 dates) for each regression
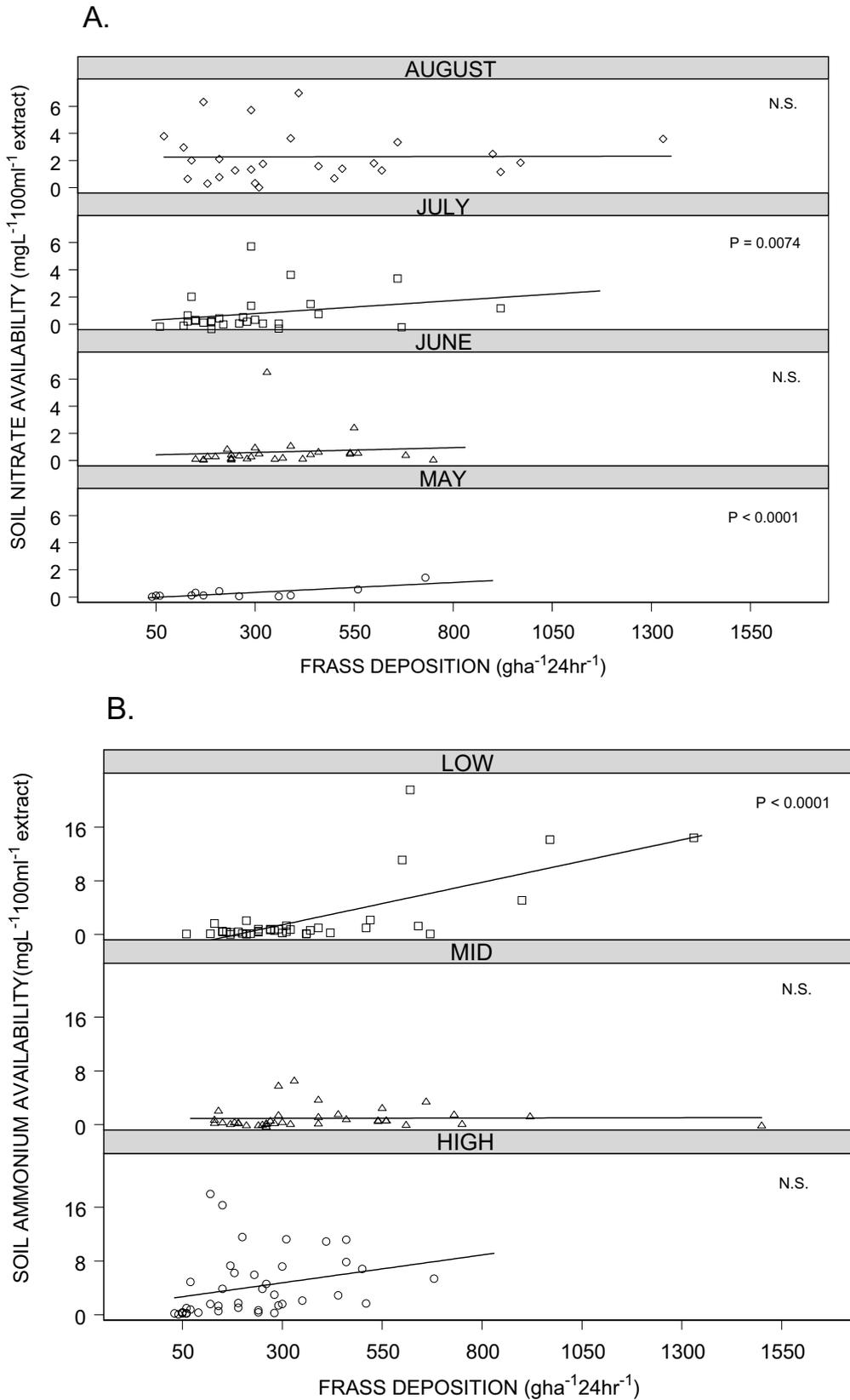
A.

B.

Fig. 8. Relationships between A) nitrate and B) ammonium availability in soil and the deposition of frass A) on four dates and B) at three elevations at the Coweeta LTER Site in North Carolina. N varies from 12 to 40 samples depending upon the number of samples in which nutrients exceeded lower limits of detection by the Carlo Erba technique

A.

B.

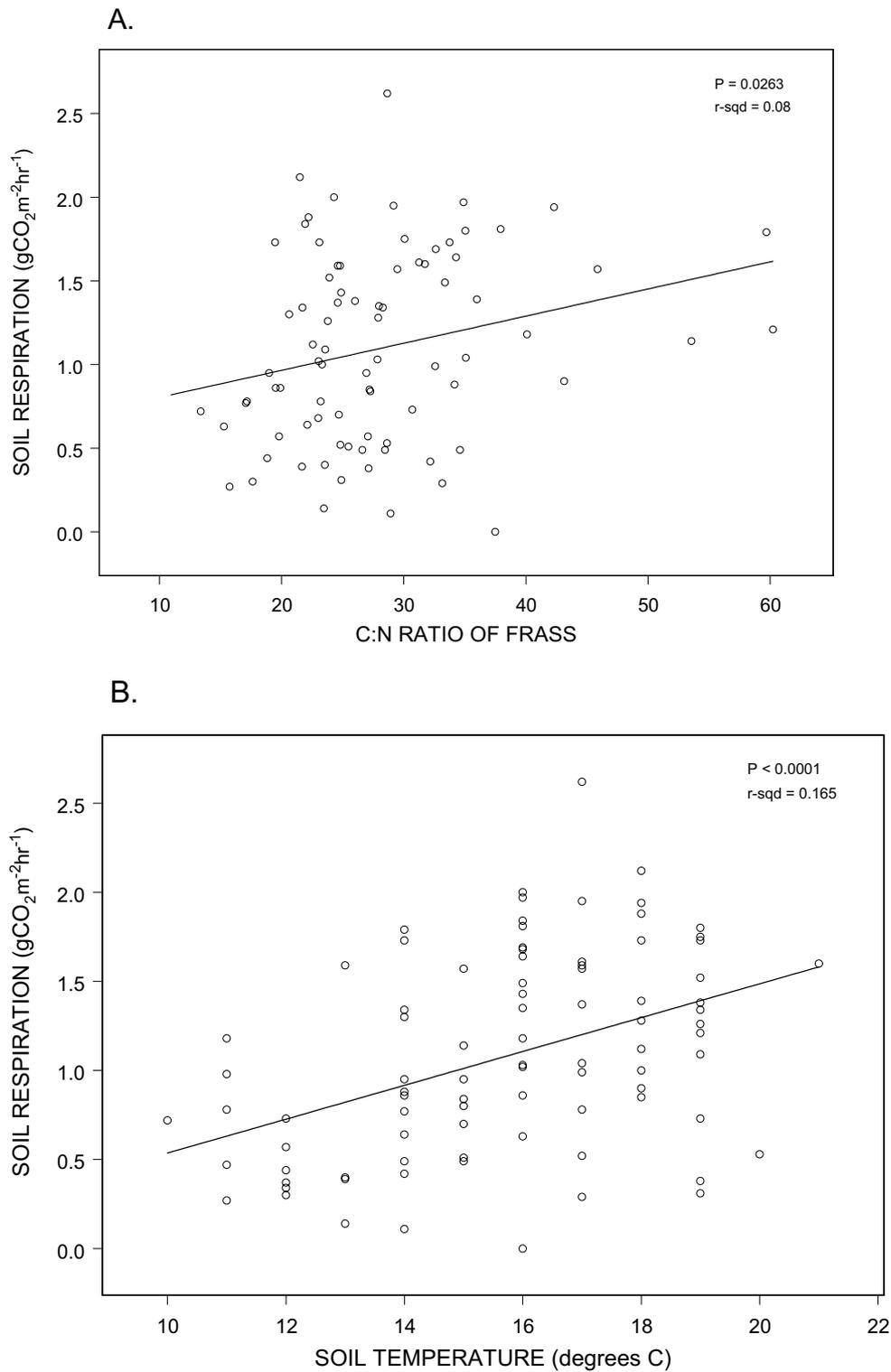**Fig. 9.** Relationships between soil respiration (g CO_2 m^{-2} hr^{-1}) and A) the C:N ratio of frass and B) soil temperature at the Coweeta LTER Site in North Carolina. N = 90 (10 samples × 3 dates × 3 elevations) for each regression. *P*-values were determined by non-parametric statistics and parametric r-squared values are provided only as an indication of the variance explained

($\chi^2 = 7.17$, d.f. = 1, P = 0.0074) and less than 1 % in June or August. Soil ammonium availability was positively related to frass deposition at low elevation only (frass*elevation interaction $\chi^2 = 17.36$, d.f. = 1, P = 0.0002, Fig. 8B), explaining 48 % of the variance in soil ammonium at low elevation ($\chi^2 = 23.72$, d.f. = 1, P < 0.0001) and less than 8 % of variance at mid or high elevation. Soil phosphate availability was unrelated to any of our estimates of frass inputs.

Relationships between frass and soil respiration

The C:N ratio of frass was the only frass factor related to soil respiration, and the relationship was weak but positive (frass C:N effect $\chi^2 = 4.93$, d.f. = 1, P = 0.0263, Fig. 9A), explaining 8 % of the variance in soil respiration. Soil temperature was a much better predictor of rates of soil respiration ($\chi^2 = 20.76$, d.f. = 1, P < 0.0001, Fig. 9B) as has been shown for previous studies at Coweeta (Coleman et al. 2002). However, even soil temperature explained only 16.48 % of the variance in soil respiration in a parametric analysis of variance components.

Discussion

Inputs of nitrogen in frass to forest soils under endemic densities of insect herbivores are relatively small (Ohmart et al. 1983). In our study, estimates of annual nitrogen deposition in frass can be made from the area under the curves in Fig. 2, assuming that we have captured the major inputs of frass during the growing season. These estimates suggest that nitrogen inputs in frass range between 0.3 and 1.1 Kg ha^{-1} yr^{-1} compared to estimates of nitrogen in autumnal litter fall of 27 to 31 Kg ha^{-1} yr^{-1} in the same forest (Risley and Crossley 1993). In other words, frass nitrogen represents around 1 to 4 % of that in annual litter fall when insect densities are at endemic levels.

Despite these low levels of nitrogen inputs, we were able to associate variation in frass deposition with variation in throughfall chemistry and the availability of soil nutrients. However, the principal message of our data appears to be that relationships between frass deposition and nutrient dynamics are variable in space and time. For example, concentrations of nitrate and ammonium in throughfall were positively related to the deposition of frass nitrogen and total frass deposition, respectively. However, these positive relationships were only evident at low elevation (Fig. 7). Differences among elevations at Coweeta include the phenology of frass deposition (Fig. 1), precipitation (Swift et al. 1979), temperature (Hoover & Crossley 1995),

and plant species composition (Reynolds & Crossley 1997). Any (or all) of these factors may influence the putative relationships between frass deposition and the nutrient content of throughfall shown in Fig. 7.

Several other studies have shown that defoliation influences nutrient concentrations in precipitation as it passes through the canopies of plants (Tukey & Morgan 1963; Seastedt & Crossley 1984; Hollinger 1986; Haines et al. 1991; Schowalter et al. 1991). Such herbivore-mediated changes in throughfall chemistry can be quite large (Kimmins 1972; Seastedt & Crossley 1984). For example, in a study of herbivores on black locust and red maple in the southern Appalachians, a nominal 8 % increase in leaf consumption resulted in a 70 % increase in leaching of potassium from foliage (Seastedt et al. 1983). There were also minor defoliation-induced increases in leaching of phosphorus. These effects were generated through experimental manipulation of endemic herbivore densities and suggest that even background levels of leaf damage can influence throughfall chemistry. However, nutrients in throughfall may actually decline following attack by herbivores. For example, feeding by aphids on Norway spruce reduces the concentrations of nitrate and ammonium in throughfall (Stadler & Michalzik 1999). In this case, high concentrations of dissolved organic carbon (sugars) in aphid honeydew are thought to fuel microbial immobilization of inorganic nitrogen in the canopy and so reduce the amount of nitrate and ammonium reaching the forest floor.

Not all studies support a strong role for leached nutrients from damaged leaves in subsequent nutrient dynamics (Hollinger 1986; Schowalter 1999; Lovett et al. 2002). Experimental defoliation of Douglas-fir saplings by the silver-spotted tiger moth had a statistically significant but ecologically minor influence on throughfall chemistry (Schowalter 1999). Likewise, an outbreak of the California oak moth did not result in increased leaching losses of nutrients from the foliage of *Quercus* spp. (Hollinger 1986). It would appear, therefore, that although defoliation can sometimes affect fluxes of nitrogen, phosphorus, potassium, and calcium to the forest floor in leachate (Seastedt & Crossley 1984, Schowalter et al. 1991), the magnitude of the changes to throughfall and their subsequent impact on ecosystem processes, are contingent on the systems under study (Schowalter 1999).

Similarly, we found that the relationships between frass deposition and the availability of nutrients in soil were variable in space and time. A positive association between frass deposition and soil nitrate was apparent during May and July, but not during June or August (Fig. 8A). The availability of soil ammonium increased with frass deposition at low elevation, but not at mid- or high elevation (Fig. 8B). Nutrients in frass

can, under some circumstances, be rapidly immobilized by soil microbes and the spatio-temporal variation in our data may represent periods (or sites) of low or high microbial immobilization. Lovett and Ruesink (1995) reported microbial immobilization of essentially all extractable nitrogen in gypsy moth frass in laboratory microcosms. In recent field experiments, Lovett and colleagues did not find increases in nutrient availability following frass deposition (Lovett et al. 2002), with most nitrogen retained in recalcitrant organic matter. Clearly, we need further studies to understand the circumstances under which nutrients in frass are (Lovett & Ruesink 1995) or are not (Swank et al. 1981; Crossley et al. 1988; Eshleman et al. 1988; Webb et al. 1995; Reynolds et al. 2000; Reynolds and Hunter 2001) substantially immobilized by microbial activity or retained within recalcitrant organic matter.

Although the relationships between frass deposition and soil nutrient availability were spatially and temporally variable, they were nonetheless moderately strong when they did occur. For example, frass deposition explained over 60 % of the variance in soil nitrate during May and 48 % of the variance in soil ammonium at low elevation (Fig. 8). In comparison, putative effects of frass deposition on soil respiration were weak. The C:N ratio of frass explained about 8 % of the variance in soil respiration with a further 16 % explained by soil temperature (Fig. 9). Rates of soil respiration at Coweeta are highly variable in space and time and influenced by a diversity of other factors including stand age, soil moisture, and plant species composition (Coleman et al. 2002). Given that soil respiration integrates a variety of biotic processes including respiration of microbes, roots, and soil fauna (Coleman & Crossley 1996), it is perhaps not surprising that links between herbivore inputs and soil respiration are weak.

Nutrient cycles are likely to respond rapidly to inputs of frass and modified throughfall because they do not require the decomposition of complex organic matter. These effects are analogous to McNaughton et al.'s (1988) "fast cycle". Herbivores may also influence ecosystem processes through a variety of "slow cycle" effects that we did not measure in our study. These include effects upon the progress of succession (Ritchie et al. 1998; Van Wijnen et al. 1999; Belovsky & Slade 2000) and changes in litter accumulation, canopy cover, soil characteristics, and the quality of litter inputs (Holland et al. 1992; Kielland et al. 1997; Kielland & Bryant 1998; Mulder 1999; Uriarte 2000).

In conclusion, we suggest that endemic densities of insect herbivores can have significant effects upon nutrient dynamics, although the effects are more variable in space and time than those associated with large insect outbreaks (Swank et al. 1981; Crossley et al. 1988;

Eshleman et al. 1988; Webb et al. 1995; Reynolds et al. 2000; Reynolds & Hunter 2001). We stress, however, that the results of this study are correlative and we have yet to demonstrate cause and effect. Although we have observed changes in nutrient dynamics in experimental studies in which we manipulated frass inputs (Reynolds & Hunter 2001), our earlier work was designed to mimic moderate levels of defoliation. Future manipulations of frass at input rates typical of endemic herbivore densities will be required to show that the relationships between frass deposition and nutrient dynamics that we have documented here are causally linked.

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