Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition

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Summary

During the decomposition of terrestrial leaf litter, the concentrations of lignin, tannin, cellulose, hemicellulose, nitrogen, and carbon are known to change. These chemical changes have been associated with subsequent colonization and activity of decomposer flora and fauna. Here, we report that chemical changes in litter during the first twelve months of decomposition are affected by macroinvertebrate activity. Moreover, chemical changes are associated most closely with the activities of invertebrate predators. Using litter bags that either excluded (fine mesh) or allowed access by (coarse mesh) macroinvertebrates, we followed the concentrations of lignin, tannin, cellulose, hemicellulose, nitrogen, and carbon in the litter of Liriodendron tulipifera, Quercus prinus, and Rhododendron maximum in a North Carolina forest ecosystem. We also compared chemical changes in these litters at a riparian site and an upland site within the forest. The exclusion of macroinvertebrates decreased concentrations of nitrogen and total phenolics in the litter of L. tulipifera, increased concentrations of cellulose and condensed tannin in Q. prinus litter, and increased the concentrations of condensed tannin in R. maximum litter in the riparian zone. Although fine mesh bags excluded most macroinvertebrates, the greatest effects of exclusion were upon ants and spiders, not macroinvertebrate decomposers. Our data therefore suggest that predator-mediated changes in the decomposer communities were responsible for observed shifts in litter chemistry. Predator effects on litter chemistry were likely mediated by their interactions with fungivorous and bacterivorous fauna. For example, Collembola populations were 34% higher in litter bags from which macroinvertebrates were excluded. Litter chemistries also differed between the riparian and upland sites. For both L. tulipifera and R. maximum, effects of habitat were limited to higher concentrations of condensed tannin in the upland site. In contrast, habitat effects upon the litter chemistry of Q. prinus were pervasive. Specifically, Q. prinus litter in the upland habitat exhibited slower increases in lignin, more stable concentrations of cellulose, slower increases in hemicellulose, higher concentrations of total phenolics, and higher concentrations of hydrolysable tannins than did litter in the riparian habitat. Overall, our data provide the first evidence that predators in the litter of deciduous forests can influence the chemistry of litter during the decomposition process.

Key words: macroinvertebrates, decomposition, predation, litter chemistry, lignin, tannin, leaf litter

Introduction

The chemistry of leaf litter is fundamental to its decomposition and the cycling of nutrients in forest systems (Aerts and de Caluwe 1997; Hättenschwiler and Vitousek 2000). The chemical components of leaf litter that influence decomposition and nutrient dynamics include lignin (Fogel and Cromack 1977; Meentemeier 1978; Berg et al. 1984; Aber et al. 1990), tannins and other phenolics (Basaraba 1964; Davies 1971;
Baldwin et al. 1983; Gallardo and Merino 1992), cellulose (Berg et al. 1984; McClougherty and Berg 1987; Muller et al. 1988) and nitrogen and its ratio with lignin, tannin, and carbon (Melillo et al. 1982; Boerner 1984; Blair 1988; Tian et al. 1992; Enriquez et al. 1993). It is also well established that the activities of certain invertebrates in litter and soil can increase the rate of litter decomposition and nutrient cycling (Vossbrink et al. 1979; Douce and Crossley 1982; Seastedt and Crossley 1983; Whitford and Parker 1989; Reddy 1992; Hasegawa and Takeda 1996; Irmler 2000). Litter chemistry and the activities of invertebrate decomposers are linked because chemistry is considered to be one of the major determinants of invertebrate colonization and comminution of litter (Satchell and Low 1967; Anderson 1973; Maity and Joy 1999; Zimmer and Topp 2000).

The chemistry of leaf litter is highly dynamic during the decomposition process and concentrations of simple phenolics, tannins, cellulose, hemicellulose, and lignin are known to change during decomposition (Berg et al. 1982). In some cases, tannins and phenolics are lost rapidly from decomposing leaf litter (Baldwin and Schultz 1984; Pereira et al. 1998; Schofield et al. 1998). However, relative concentrations of some phenolics may increase during decomposition depending upon their chemical structure (Gallet and Lebreton 1992) and the ability of microbes to metabolize those structures (Sugai and Schimel 1993).

Changes in phenolic and lignin concentrations during early stages of decomposition are important because they can influence subsequent rates of decomposition at later stages (Wilson et al. 1986). Effects of initial chemistry on the subsequent trajectory of decomposition are based in part upon interactions with detritivores (Valiela et al. 1984; Lagerloef and Andres 1985; Pereira et al. 1998). For example, low C:N ratios and low concentrations of polyphenolics favor consumption by, and population growth of, some invertebrate decomposers (Satchell and Low 1967; Maity and Joy 1999; Zimmer and Topp 2000). Indeed, the loss, transformation or leaching of phenolic compounds during decomposition can have a range of effects upon soil and plant communities including subsequent colonization of litter by arthropods (Anderson 1973; Pereira et al. 1998), rates of nitrogen mineralization and immobilization (Northup et al. 1995; Schimel et al. 1996, 1998), the formation of humic acids (Schnitzer et al. 1984), iron sequestration and deficiency in soil (Julian et al. 1983; Kuiters and Mulder 1993) and allelopathic effects upon other plant species (Gallet 1994; Wallstedt et al. 2000).

Given an initial chemical composition at the beginning of the decomposition process, what factors are likely to influence the trajectory of litter chemistry (changes in the relative concentrations of lignin, phenolics, and nitrogen) during decomposition? The availability and activity of microbial decomposers will obviously play a major role (Benoit and Starkley 1968; Azhar et al. 1989; Sugai and Schimel 1993). However, other factors that might influence the direction and magnitude of chemical change include the activities of litter and soil invertebrates and the habitat in which the decomposition is taking place. To our knowledge, the relative impacts of macroinvertebrates and habitat on chemical changes during the decomposition of litter have not been explored previously.

Macroinvertebrates are considered to play an important role in the decomposition of plant material (Prins 1983; Silva et al. 1985; Garay et al. 1986; Bertrand and Lumaret 1992; Curry and Byrne 1997; Paoletti and Hassall 1999; Irmler 2000), with particularly strong effects at fine spatial and temporal scales (Lavelle et al. 1993). By the processes of fragmentation and comminution, macroinvertebrates can influence decomposition through their effects upon fungal and bacterial populations (Anderson and Inseon 1983; Scheck 1993). In some cases, effects of macroinvertebrate exclusion on decomposition have been shown to vary with the species of leaf litter (Spain and Feuvre 1987), presumably because of their differential impacts upon the microbial flora. However, little is known about the potential of predatory macroinvertebrates within litter to influence decomposition processes through their impacts upon microarthropods. We explore those effects here.

In addition to effects of fauna, the same litter can decompose at different rates based upon the environment in which it decomposes (Holland and Coleman 1987). Site-based factors affecting decomposition include pH (Kok and van der Velde 1994; Verhoeven and Toth 1995), redox conditions (Valiela et al. 1984), and soil temperature and moisture (Meentemeyer 1978; Douce and Crossley 1982; Seastedt et al. 1983; Hijii 1994; Aerts 1997). In some cases, environmental factors may interact with invertebrate abundance to influence rates of decomposition (Reddy 1984; Steinberger et al. 1984; Blair and Crossley 1988; Cepeda and Whitford 1989; Frith and Frith 1990). For example, effects of macroinvertebrate exclusion upon the decomposition of Nymphaea alba and Betula pubescens leaves depend upon the pH of the environment (Kok and van der Velde 1994). Similarly, densities of arthropods and nematodes within desert leaf litter can depend upon the availability of rainfall (Whitford et al. 1981; Steinberger and Ben-Ythak 1990).

Here, we consider the relative roles of macroinvertebrates and local habitat on chemical changes during litter decomposition. We also consider interactions between macroinvertebrates and habitat. Our study was designed to answer three key questions:
1. Do macroinvertebrates influence the chemical trajectory of decomposing leaf litter?
2. Do effects of macroinvertebrates on litter chemistry vary with the quality (= species) of the litter?
3. Do the effects of macroinvertebrates on litter chemistry vary with the site of decomposition?

Because macroinvertebrate predators responded to exclusion more than any other group, our data provide us with the opportunity to explore predator-mediated changes in decomposition processes.

Materials and Methods

Study site
Our study was conducted at the Coweeta Hydrologic Laboratory in western North Carolina. Coweeta is in the Nantahala Mountain Range, within the Blue Ridge Physiographic Province at latitude 35° 03'N and longitude 83° 25'W (Swank and Crossley 1988). Our research site was around 750 m elevation on a north west-facing slope adjacent to Grady Branch, a tributary of Ball Creek. Soils at this elevation are typic and humic hapludults (Knoepp and Swank 1998). Our work was divided between a riparian plot, immediately adjacent to Grady Branch, and an upland plot, about 10 m higher in elevation and within 25 m of the creek.

Litter bags
During December of 1999, we collected fresh litter of three dominant tree species at Coweeta; Liriodendron tulipifera, Quercus prinus, and Rhododendron maximum. Litters were collected from the experimental site (upland area, above) and chosen to represent three “qualities” based upon previously published rates of decay; fast decay (L. tulipifera), intermediate decay (Q. prinus) and slow decay (R. maximum) (Hoover and Crossley 1995). Litter was brought to the laboratory and air-dried at ambient temperatures for four weeks. For each species, we constructed 48 litter bags, 15 cm by 10 cm. Half of the bags were of fine mesh (1.5 mm) plastic window screen to exclude macroinvertebrates. The other half were coarse mesh (15 mm) plastic netting to allow access by macroinvertebrates. Using litter bags of varying mesh size remains the standard experimental procedure for determining the effects of invertebrates upon litter decomposition (e.g. Vossbrink et al. 1979; House and Stinner 1987; Spain and Feuvre 1987; Reddy 1992; Tian et al. 1992; Argyropoulou et al. 1993; Judas et al. 1995; Curry and Byrne 1997; Irm. ler 2000). Twelve bags of each mesh size for each species were returned to each research plot ( riparian and upland) on January 12 2000. Overall, we placed 144 litter bags at our research site (2 plots × 3 species × 2 mesh sizes × 12 bags).

Collection and analysis
Every three months for a total of twelve months, we collected three litter bags (replicates) of each species and mesh size from each of the plots. Collections were made on April 17, 2000, July 13, 2000, October 15, 2000, and January 15, 2001. Litter bags were sealed individually in plastic bags and returned to the laboratory for analysis. Macroinvertebrates were removed from samples using modified Tullgren funnels (Mallow and Crossley 1984) and hand-sorting of the largest specimens. We have also made preliminary counts of Collembola. Litter was dried at 65 °C for three days and weighed. Samples were then ground to a fine powder in a Wiley mill and stored at −80 °C for chemical analyses.

Carbon and nitrogen concentrations were determined on an Alpkem flow-injector analyzer and are reported as percent dry weights. Cellulose, hemicellulose and lignin concentrations were estimated by sequential neutral detergent/acid detergent digestion on an Ankom fiber analyzer and are also reported as percent dry weights. We conducted three separate analyses for phenolics; condensed tannins, hydrolysable tannins, and total phenolics. Samples for tannin analysis were extracted in 70 % acetone with 1 mM ascorbic acid and evaporated under reduced pressure to provide aqueous extracts. Given concerns about the purity of tannic acid as a standard in tannin analysis (Hagerman and Butler 1991), sample extracts were tested against tannin standards (Forkner and Hunter 2000) prepared from pooled litter (all three species combined). The standards were prepared on each sampling date by acetone/ascorbate extraction as above and then lyophilized to provide a bulk tannin powder. Condensed tannins were estimated as proanthocyanidins using methods described in Rossiter et al. (1988). Hydrolysable tannins were estimated using a potassium iodate technique developed by Bate-Smith (1977) and modified by Schultz and Baldwin (1982). Total phenolics were estimated using the Folin-Denis assay (Swain 1979). Because the phenolics in each species of litter were compared against a common tannin standard, the values reported reflect relative indices of concentration, not absolute values, and can exceed 100%.

Statistical analyses
Neither the litter chemistry data nor the counts of macroarthropods met assumptions of normality. Consequently, all analyses were carried out using generalized linear models (Proc Genmod, SAS Inst. 1996) with
Fig. 1. Concentrations of nitrogen in the litter of A) Liriodendron tulipifera, B) Quercus prinus, and C) Rhododendron maximum, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.

Fig. 2. Concentrations of carbon in the litter of A) Liriodendron tulipifera, B) Quercus prinus, and C) Rhododendron maximum, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.
Fig. 3. Carbon to nitrogen ratios in the litter of A) *Liriodendron tulipifera*, B) *Quercus prinus*, and C) *Rhododendron maximum*, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.

Fig. 4. Concentrations of lignin in the litter of A) *Liriodendron tulipifera*, B) *Quercus prinus*, and C) *Rhododendron maximum*, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.
Table 1. Results of generalized linear models analyzing the effects of time, macroinvertebrate exclusion (mesh), and habitat (riparian or upland) on the chemistry and mass of decomposing litter. Asterisks represent statistical significance (*<0.01, **<0.001, ***<0.0001) and NS represents not significant.

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poisson distributions, log link functions, and scaled deviance for the hyper-dispersion of data. In all cases, the statistical models converged to provide good fits to the data. 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). Given that we analyzed multiple indices of chemical change for each plant species, p-values were adjusted by Sidak's Multiplicative Inequality (SAS Inst. 1996) to provide conservative estimates of significance (p-values of less than 0.01).

Results

As expected, the concentrations of lignin, phenolics, cellulose, hemicellulose, nitrogen and carbon in litter changed during the 12 months of decomposition (Table 1). Nitrogen concentrations generally increased (Fig. 1), carbon concentrations were more stable (Fig. 2), and so the decline in C:N ratio of all litter species (Fig. 3) can be attributed primarily to relative increases in nitrogen. The concentration of lignin increased over time (Fig. 4), presumably as less recalcitrant material was lost from the litter. Cellulose fractions declined steadily in *L. tulipifera* litter, while cellulose in both *Q. prinus* and *R. maximum* initially declined and then increased in concentration (Fig. 5). The concentrations of hemicellulose began increasing after six months (Fig. 6), while total phenolics generally decreased (Fig. 7). Changes in the concentrations of condensed tannin (Fig. 8) and hydrolysable tannin (Fig. 9) varied among litter species and exhibited no consistent pattern over time.

Effects of macroinvertebrate exclusion and habitat (riparian versus upland) on litter chemistry varied with the species of plant litter (Table 1). For *L. tulipifera*, the exclusion of macroinvertebrates decreased the concentration of nitrogen ($\chi^2 = 9.80$, d.f. = 1, $p = 0.0017$, Fig. 1a) and decreased the concentration of total phenolics ($\chi^2 = 10.06$, d.f. = 1, $p = 0.0015$, Fig. 7a) in leaf litter. For *Q. prinus*, the exclusion of macroinvertebrates mitigated the decline in cellulose concentration at month 9 in the decomposition process (mesh*date interaction $\chi^2 = 20.81$, d.f. = 4, $p = 0.0003$, Fig. 5b). Exclusion also resulted in a rapid increase in the concentration of condensed tannin in upland *Q. prinus* litter (mesh*date*habitat interaction $\chi^2 = 26.26$, d.f. = 4, $p < 0.0001$, Fig. 8b). In the litter of *R. maximum*, concentrations of condensed tannin in litter increased in all treatments early in decomposition, except in litter exposed to macroinvertebrates in the riparian zone (mesh*date*habitat interaction $\chi^2 = 26.58$, d.f. = 4, $p < 0.0001$, Fig. 8c).

![Fig. 5. Concentrations of cellulose in the litter of A) *Liriodendron tulipifera*, B) *Quercus prinus*, and C) *Rhododendron maximum*, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.](image-url)
Fig. 6. Concentrations of hemicellulose in the litter of A) *Liriodendron tulipifera*, B) *Quercus prinus*, and C) *Rhododendron maximum*, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.

Fig. 7. Concentrations of total phenolics in the litter of A) *Liriodendron tulipifera*, B) *Quercus prinus*, and C) *Rhododendron maximum*, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Values were generated against tannin standards from pooled litter and represent indices of concentration relative to the bulk standards. Data are the means of three replicates and bars represent standard errors.
Fig. 8. Concentrations of condensed tannin in the litter of A) Liriodendron tulipifera, B) Quercus prinus, and C) Rhododendron maximum, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Values were generated against tannin standards from pooled litter and represent indices of concentration relative to the bulk standards. Data are the means of three replicates and bars represent standard errors.

Fig. 9. Concentrations of hydrolysable tannin in the litter of A) Liriodendron tulipifera, B) Quercus prinus, and C) Rhododendron maximum, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Values were generated against tannin standards from pooled litter and represent indices of concentration relative to the bulk standards. Data are the means of three replicates and bars represent standard errors.
Table 2. Total macroarthropods and Collembola extracted from 144 litter bags collected quarterly during a twelve-month study of litter decomposition. Totals are for 24 bags each of *Liriodendron tulipifera*, *Quercus prinus*, and *Rhododendron maximum* litter from both riparian and upland habitats. Note that macroinvertebrates can move both in and out of coarse mesh bags so that counts represent relative activities, not total numbers that visited bags during the experiment.

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<td>Chilopoda</td>
<td>5</td>
<td>7</td>
<td>12</td>
</tr>
<tr>
<td>Diptera</td>
<td>7</td>
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</tr>
<tr>
<td>Coleoptera</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Collembola</td>
<td>877</td>
<td>1175</td>
<td>2052</td>
</tr>
</tbody>
</table>

The influence of habitat on the chemistry of decomposition was also variable among plant species (Table 1). For *L. tulipifera*, condensed tannin concentrations increased early in decomposition in the upland habitat, irrespective of macroinvertebrate access to litter (date*habitat interaction $\chi^2 = 74.60$, d.f. = 4, $p < 0.0001$, Fig. 8a). The chemistry of *Q. prinus* litter was particularly sensitive to plot location, with significant effects of habitat, or date by habitat interactions, on lignin, cellulose, hemicellulose, hydrolysable tannin, and total phenolics (Table 1). Specifically, litter in the upland habitat exhibited slower increases in lignin (date*habitat $\chi^2 = 17.10$, d.f. = 4, $p = 0.0018$, Fig. 4b), more stable concentrations of cellulose (date*habitat $\chi^2 = 18.49$, d.f. = 4, $p = 0.0010$, Fig. 5b), slower increases in hemicellulose (date*habitat $\chi^2 = 14.41$, d.f. = 4, $p = 0.0061$, Fig. 6b), higher concentrations of total phenolics (habitat $\chi^2 = 10.84$, d.f. = 1, $p = 0.0010$, Fig. 7b), and higher concentrations of hydrolysable tannins (habitat $\chi^2 = 13.89$, d.f. = 1, $p = 0.0002$, Fig. 9b) than did litter in the riparian habitat. For *R. maximum*, effects of habitat on litter chemistry were restricted to the date by mesh by habitat interaction on condensed tannin described previously.

The number of macroinvertebrates recovered in litter bags was quite low (Table 2), and it was not possible to analyze most taxonomic groups individually. Given that macroinvertebrates can both enter and leave coarse mesh bags, we assume that the numbers we recovered underestimate the densities of macroinvertebrates responsible for treatment effects. Rather, our counts provide some measure of the relative activities of macroinvertebrates within bags. Average counts of all macroinvertebrates combined, predominantly ants and spiders, were nearly three times higher in coarse mesh bags than

Fig. 10. Mass remaining in the litter of A) *Liriodendron tulipifera*, B) *Quercus prinus*, and C) *Rhododendron maximum*, during the first twelve months of decomposition. Litter bags were either coarse mesh (15 mm) or fine mesh (1.5 mm) in a riparian (Rip) or upland (Up) site. Data are the means of three replicates and bars represent standard errors.
in fine mesh bags. Means ± standard errors were 1.94 ± 0.68 and 0.68 ± 0.11 per bag for coarse and fine mesh bags, respectively (mesh $\chi^2 = 8.70$, d.f. = 1, $p = 0.0032$). Collembola populations in fine mesh bags were 34% higher than in coarse mesh bags (Table 2) suggesting that the exclusion of ants and spiders (Table 2) resulted in higher populations of fungivores. Average densities of macroinvertebrates per litter bag were also higher in the upland plot (1.65 ± 0.69) than in the riparian plot (0.75 ± 0.13) and it is therefore possible that some habitat effects on litter chemistry (above) were caused by the availability of macroinvertebrates to colonize litter. However, the only significant interactions between mesh size and habitat were for condensed tannin concentrations (Table 1).

The exclusion of macroinvertebrates reduced the rate of mass loss of L. tulipifera litter ($\chi^2 = 6.59$, d.f. = 1, $p = 0.0103$, Table 1, Fig. 10a). Rates of mass loss of Q. prinus litter were unrelated to either macroinvertebrate exclusion or habitat (Table 1, Fig. 10b) over the time periods measured here. Mass loss of R. maximum litter was also unrelated to macroinvertebrate exclusion over the first twelve months of decomposition, but depended in part upon habitat. Rates of mass loss were initially slower in the riparian plot but, by the end of twelve months, were faster in the riparian than in the upland plot (date*habitat $\chi^2 = 22.67$, d.f. = 4, $p < 0.0001$, Table 1, Fig. 10c).

Discussion

Several studies have demonstrated that the chemistry of leaf litter influences subsequent colonization by, and activity of, invertebrate decomposers (Satchell and Low 1967; Anderson 1973; Maity and Joy 1999; Zimmer and Topp 2000). Here, we show that the reverse may also be true. Our data suggest that the activity of macroinvertebrates during the first twelve months of decomposition can influence temporal changes in litter chemistry. For all three species of litter that we used in our experiments, macroinvertebrates had detectable effects upon some measure of litter chemistry (Table 1). However, the particular effects of macroinvertebrates on litter chemistry varied among plant species. For example, macroinvertebrates appeared to increase concentrations of nitrogen and total phenolics in the litter of L. tulipifera (Figs. 1a and 7a, respectively). In contrast, macroinvertebrates decreased concentrations of cellulose and condensed tannin in Q. prinus litter (Figs. 5b and 8b, respectively). Finally, in R. maximum litter in the riparian zone, macroinvertebrates appeared to decrease concentrations of condensed tannin (Fig. 8c).

There are several reasons to expect that macroinvertebrate effects on the chemistry of leaf litter would be specific to the species of litter. First, previous studies have shown that effects of macroinvertebrate exclusion on mass loss vary with the species of leaf litter (Spain and Feuvre 1987) and we show the same result here. In our study, macroinvertebrates increased mass loss only on L. tulipifera litter, with no effects upon the other species (Fig. 10). Second, initial nitrogen, phenolic and cellulose chemistries of our three species varied markedly (Figs. 1, 5–9) and any macroinvertebrate-mediated changes in litter chemistry will have been constrained to some degree by starting conditions of the litter. Moreover, qualitative variation in phenolic chemistry among litter species is likely to influence chemical changes that occur during decomposition (Baldwin and Schultz 1984; Sugai and Schimel 1993; Gallet and Lebreton 1995; Pereira et al. 1998; Schofield et al. 1998). Finally, the dominant effects of macroinvertebrates upon litter decomposition are generally considered to be indirect, acting through changes in the densities of microinvertebrates and microbial decomposers (Anderson and Inseon 1983; Scheu 1993). For example, in meadows in Poland, the exclusion of macroinvertebrates influences the accumulation and distribution of soil carbon during decomposition (Kajak 1997, 2000). In this case, macroinvertebrate effects are thought to result from the dual processes of reduced comminution and predator-induced changes in the relative abundance of fungivorous and bacterivorous invertebrates (Kajak et al. 2000). In our study, spiders and ants were dominant members of the macroarthropod assemblage recovered from litter bags (Table 2), suggesting that predator-mediated effects upon decomposition may have been the most significant. Assuming that our litter species supported different food webs of floral and faunal decomposers (Moore 1988; Siepel 1990; Chen and Wise 1999; Hansen 2000; Johnston 2000), then effects of macroinvertebrate exclusion on chemistry may well have operated by changes in these food webs. In support of this hypothesis, Collembola populations were 34% higher in litter bags from which macroinvertebrates (particularly spiders and ants) were excluded (Table 2).

We also found that the chemistry of decomposing litter varied between the riparian and upland habitat. For both L. tulipifera and R. maximum, habitat effects were limited to higher concentrations of condensed tannin in the upland site (Figs. 8a and 8c, respectively). In contrast, habitat effects upon the litter chemistry of Q. prinus were pervasive. Specifically, Q. prinus litter in the upland habitat exhibited slower increases in lignin (Fig. 4b), more stable concentrations of cellulose (Fig. 5b), slower increases in hemicellulose.
(Fig. 6b), higher concentrations of total phenolics (Fig. 7b), and higher concentrations of hydrolysable tannins (Fig. 9b) than did litter in the riparian habitat. At present, we do not know why the chemistry of Q. prinus litter is so much more sensitive to microhabitat than is the chemistry of the other litter species. While it is possible that differences in the abundance of macroinvertebrates between the upland and riparian site contributed to observed habitat effects upon litter chemistry, the data suggest that other site-based factors may be more important. If macroinvertebrate abundance was the dominant site factor operating, we might expect to see significant habitat*mesh interactions, whereby the effect of habitat on chemistry was greater in coarse mesh (macroinvertebrate accessible) than in fine mesh bags (macroinvertebrates excluded). Significant habitat*mesh interactions were limited to the condensed tannin chemistries of Q. prinus and R. maximum litter, and absent from the majority of habitat effects (Table 1). Although interactions between invertebrate decomposers and local microclimate have been shown to influence decomposition in previous studies (Reddy 1984; Steinberger et al. 1984; Blair and Crossley 1988; Cepeda and Whitford 1989; Frith and Frith 1990), they do not appear to be responsible for variation in litter chemistry in our study. Alternative site factors for future study include soil pH (Kok and van der Velde 1994; Verhoeven and Toth 1995), redox conditions (Valiela et al. 1984), and soil temperature and moisture (Meentemeyer 1978; Douce and Crossley 1982; Seastedt et al. 1983; Hijii 1994).

In summary, our data demonstrate that macroinvertebrates and local site conditions can both contribute to changes in the chemistry of litter during decomposition. While our results are limited to the first twelve months of decomposition, they are significant because early changes in the chemistry of litter are known to influence a range of subsequent ecological processes including colonization of litter by microarthropods (Anderson 1973; Pereira et al. 1998), rates of nitrogen mineralization and immobilization (Northup et al. 1995; Schimmel et al. 1996 1998), the formation of humic acids (Schnitzer et al. 1984), iron sequestration and deficiency in soil (Julian et al. 1983; Kuiters and Mulder 1993) and allelopathic effects upon other plant species (Gallet 1994; Wallstedt et al. 2000). The degree to which macroarthropod-mediated changes in litter chemistry influence these processes will be the subject of future work in this system.

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