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The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics

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We examined how plant genetic variation and a common herbivore (the leaf-galling aphid, *Pemphigus betae*) influenced leaf litter quality, decomposition, and nutrient dynamics in a dominant riparian tree (*Populus spp*.). Based on both observational studies and a herbivore exclusion experiment using trees of known genotype, we found four major patterns: 1) the quality of galled vs non-galled or gall-excluded litter significantly differed in the concentration of condensed tannins, lignin, nitrogen and phosphorus; 2) the difference in litter quality resulted in galled litter decomposing at rates 34 to 40% slower than non-galled litter; 3) plant genotype and herbivory had similar effects on the magnitude of decomposition rate constants; and 4) plant genotype mediated the herbivore effects on leaf litter quality and decomposition, as there were genotype-specific responses to herbivory independent of herbivore density. In contrast to other studies that have demonstrated accelerated ecosystem properties in response to arthropod herbivory, our findings argue that herbivore-induced secondary compounds decelerated ecosystem properties though their "after-life" effects on litter quality. Furthermore, these data are among the first to suggest that genotype-specific responses to herbivores can have a major impact on decomposition and nutrient flux, which likely has important consequences for the spatial distribution of nutrients at the landscape level. Due to the magnitude of these effects, we contend that it is important to incorporate a genetic perspective into ecosystem studies.

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Introduction

Insect herbivory may influence terrestrial ecosystem-level processes in many ways. Though consuming ~10–20% of annual above ground net primary productivity (ANPP) in any given, non-outbreak year (Cyr and Pace 1993, Cebrian 1999), the effects of herbivore-altered litterfall, microclimate, throughfall, honeydew and frass can make important contributions to soil nutrient dynamics (Seastedt and Crossley 1984, Bardgett and Wardle 1998, Schowalter 2000, Hunter 2001, Lovett et al. 2002). Alterations in plant community composition due to preferential foraging on nutrient-rich plant species may also lead to changes in ecosystem function after herbivory through a variety of mechanisms (Pastor and Cohen 1997, Ritchie et al. 1998, Wardle et al. 2002, Bardgett and Wardle 2003). The impacts of insect-induced alterations of leaf litter, however, may have a more consistent impact on ecosystem-level processes as chronic herbivory is more common than outbreaks

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(Mason 1987, Price et al. 1990, Hunter 1995) and leaf litter represents a regular and important source for internal nutrient cycling in forest ecosystems (Attiwell and Adams 1993, Schowalter 2000, Hunter 2001). Herbivore alterations of leaf litterfall timing (Blundell and Peart 2000) or chemical quality, via interruptions in reabsorption or induction of secondary compounds, can result in altered leaf litter decomposition and possibly nutrient cycling (Risley 1986, Findlay et al. 1996, Ritchie et al. 1998, Chapman et al. 2003).

Induction of plant secondary compounds is an important mechanism that plants can utilize to cope with insect herbivory (Karban and Baldwin 1997, Bardgett and Wardle 1998, Gatehouse 2002). Herbivore-induced secondary compounds, especially polyphenols (Hättenschwiler and Vitousek 2000, Nykänen and Koricheva 2004), that are produced after insect feeding may be retained with leaf abscission and affect subsequent decomposition processes. Such "afterlife" effects have been shown to slow litter decomposition (Choudhury 1988, Findlay et al. 1996), which could impact nutrient cycling rates within the ecosystem. While the effects of plant secondary compounds, including induced defenses, on leaf litter decomposition have been demonstrated (Horner et al. 1988, Findlay et al. 1996, Grime et al. 1996, Northup et al. 1998, Schimel et al. 1998), variation in response to herbivory and interactions with individual plant genotype are much less appreciated. A genetic perspective such as this is important because it begins to place ecosystem science within a genetic and evolutionary framework (Loehle and Pechman 1988, Van der Putten et al. 2001).

Although the effects of genetic variation in plants on ecosystem-level processes are now beginning to be recognized (Driebe and Whitham 2000, Treseder and Vitousek 2001, Lindroth et al. 2002, Madritch and Hunter 2002, 2004, Fischer et al. 2004, Schweitzer et al. 2004), here we addressed how interactions between plant genotype and herbivory can modify the impacts of plant genetic variation on ecosystem-level processes. Natural hybrid zones are ideal for examining the relationships between plant genotype and plant herbivory as natural plant hybridization commonly occurs (Rieseberg and Carney 1998), and hybrids express high genetic variation in traits such as secondary chemistry (Orians 2000, Orians et al. 2000) and resistance to herbivory (Strauss 1994, Fritz et al. 1998, Fritz 1999). *Populus* (cottonwood) species commonly hybridize whenever species boundaries overlap (Eckenwalder 1984a, 1999), and the leaf-galling aphid, *Pemphigus betae*, is commonly associated with these hybrids; on average, *P. betae* is 28-fold more abundant in these hybrid zones than adjacent pure zones (Whitham 1989, Floate et al. 1997). Furthermore, some cottonwood hybrids possess natural resistance traits that influence the distribution of *P. betae* (Paige and Capman 1993). We utilized this natural variation in cottonwood resistance to *P. betae* to examine the interactive effects of *P. betae* galls and plant genotype on leaf litter decomposition and nutrient dynamics. Specifically, we addressed the following questions: 1) does herbivory by a galling aphid impact leaf litter quality, decomposition rate and nutrient release? and 2) do individual cottonwood genotypes differ in their response to herbivory?

Methods

Study sites and organisms

To address these questions, we utilized a 13 km hybrid zone along the Weber River, Utah, USA (41.2°N, 112.0°W) with natural stands of hybrid (backcross) cottonwood (*Populus fremontii* L. × *P. angustifolia* James). *Populus fremontii* and *P. angustifolia* naturally hybridize whenever the two species come in contact, creating hybrid zones at the edges of their elevational boundaries (Eckenwalder 1984a, 1984b). The hybrid zone is composed of F_1 hybrids and complex backcrosses, as well as both pure species, creating stands of trees with high genetic variation (Keim et al. 1989, Martinsen et al. 2001).

Pemphigus betae (Homoptera:Aphididae) is a gall-forming aphid species with a complex host-alternating life cycle, which utilizes *Populus* spp. as the primary host plant (Whitham 1978, Moran and Whitham 1988a, 1988b). In early spring, the stem-mothers (i.e. fundatrices) initiate hollow galls at the base of expanding leaf blades where they parthenogenetically produce up to several hundred progeny, which feed via the leaf phloem until June or July of the same year. The result of this four to five month association with the trees is that the galls become mobilizing sinks of the plants resources (Larson and Whitham 1991), and affect the diversity of associated bird, arthropod and fungal communities (Dickson and Whitham 1996, Waltz and Whitham 1997). We predicted that this long term association could also affect leaf and litter chemistry, which can have "afterlife" affects on subsequent leaf litter decomposition and nutrient release.

Observational studies

To determine if leaf-galling herbivores altered leaf litter quality and decomposition across sites, we established litter bag decomposition studies in 1997 and 1999 that lasted for 16 and 18 months, respectively. These two observational studies allowed the assessment of both the interannual variation in decomposition rates and nutrient dynamics, as well as the interactions of herbivory and site on these processes for each year separately. Litter was collected for both years from 6 to 10 naturally

resistant (to *P. betae*) and 6 to 10 naturally susceptible backcross hybrid cottonwoods in the field. We focused our studies on naturally occurring hybrid genotypes in the field as *P. betae* is concentrated on hybrid trees throughout the western USA (Whitham 1989, Floate et al. 1997). We collected leaf litter in mesh bags (2 mm openings) tied around branches at the time of leaf fall, and pooled all genotypes. Because galled leaves begin senescing earlier than non-galled leaves (Williams and Whitham 1986), galled litter was stored in the dark at room temperature until the non-galled litter senesced. Three to five grams of airdried litter from both treatments were placed separately in mesh bags, and randomly placed on the ground surface in three field sites with steel nails. The litterbags had 3 mm openings on the top and 0.5-mm on the bottom to maximize colonization by soil fauna, but minimize loss of litter due to leaf fragmentation. For each study, we placed litterbags from the two treatments (i.e. galled and non-galled litter) in three field sites that were representative of microclimate variation and range of possible habitat encountered by *P. betae* along the drainage. Five litter bags of each type for each of two collection dates were placed at each of these sites (2 treatments $\times 3$ sites $\times 2$ collection dates $\times 5$ replicates; $n = 60$ total litter bags per study). However, in 1999 one of these sites was vandalized, reducing the number of study sites to two.

Subsamples of each litter type were retained as "initials" for both studies to assess litter chemical parameters before decomposition in the field and to evaluate interannual variation in leaf litter chemistry. After each collection date, the litterbags were removed from the field and all soil and biotic contaminants were removed by hand. The samples were then airdried in paper sacks, individually weighed and then ground through a 40 mesh screen with a Wiley Mill. Subsamples of the ground leaf material were separately ashed (500°C for 1 h) and oven-dried (70°C for 48 h). All final weights are expressed on an ash-free, oven-dry mass basis (AFODM). Nutrient dynamics were assessed for each sample by examining total nitrogen (N) and phosphorus (P) concentrations in leaves initially and after decomposition at each collection date using methods described below. The remainder of the ground initial litter material was stored in a −80°C freezer until condensed tannin and lignin analyses could be conducted.

Herbivore exclusion experiment

In 2000, we performed an experiment to prevent galling-aphid colonization on aphid-susceptible trees to determine if the presence of galls induces differences in leaf litter chemistry or if the aphid stem-mother simply chooses leaves with particular leaf chemistries. The natural history of these organisms allows prevention of colonization by denying the stem-mother access to branches from their over-wintering sites on the trunk. By placing a sticky barrier, Tangle-Trap® (Grand Rapids, MI, USA) around a branch, we prevented colonization of the foliage on that branch. We chose 10 aphid susceptible trees at a single site in the hybrid zone (one of the same sites used in the observational experiments) and placed Tangle-Trap® on one large branch of each tree. Each treated branch was matched for size and position within the tree crown with an adjacent control branch. The barrier was applied to the chosen branches in February, just before bud-break. Each tree genotype was categorized as backcross using RFLP analyses of 35 species-specific markers (Martinsen et al. 2001). With this information, we were able to accurately discriminate among tree genotypes.

In October of the same year, we collected leaf litter from the control and gall-exclusion branches and established a 24 month decomposition experiment. Mesh bags (similar to the observational studies) were placed over gall-exclusion and control branches just before leaf senescence. Leaves were collected in the bags as they abscised from the tree every two weeks. We obtained enough galled leaf litter for the decomposition experiment from only five of the original 10 genotypes. Leaf litter was airdried and three to five grams were placed in mesh litterbags, following the same methods as in the observational decomposition studies described above. Paired bags of each herbivore exclusion treatment (i.e. galled control and gall-exclusion) were placed in randomized blocks on the ground surface in a single site of mature cottonwood forest within the hybrid zone, to minimize the effects of environment on litter decomposition and nutrient dynamics. We placed five replicates of each herbivore treatment from the five tree genotypes in the field. Bags were collected four times over a 24 month time period (5 genotype treatments $\times 2$ herbivore treatments $\times 4$ collection dates $\times 5$ replicates of each; $n =$ 200 total litter bags). Subsamples of each litter type (galled control and gall-exclusion) for all 10 original genotypes were retained as "initials" to assess their initial litter chemistries prior to decomposition. As in the observational studies, nutrient dynamics were assessed for each litterbag by measuring total N and P concentrations (on ground subsamples) in leaves initially and after decomposition at each collection date using methods described below. Condensed tannin and lignin analyses were conducted on the remaining subsamples that had been stored at −80°C (below).

Chemical analyses

We separately quantified the initial litter chemical composition for the litter types used in each study. To determine if the gall had different chemical properties

than the leaf lamina, the tissues were analyzed separately (Hartley 1998). The gall was removed from the leaf lamina, all frass and inquilines were removed, and the gall and leaf lamina tissues were then ground and analyzed. The data for each observational and experimental study are presented as galled (GL, lamina from the galled leaves only) and non-galled or gall exclusion litter (NG).

Subsamples of ground and airdried leaf litter were exhaustively extracted for condensed tannins with 70% acetone +10 mM ascorbic acid. We used the butanol-HCl method to determine condensed tannin concentrations (Porter et al. 1986), with standards purified from narrowleaf cottonwood following the methods of Hagerman and Butler (1989). We quantified absorbance on a Spectramax-Plus 384 spectrophotometer (Molecular Devices, Sunnyvale, CA, USA). We quantified lignin concentrations with the acetyl-bromide method using an NIST certified pine standard (Ilyama and Wallis 1990). Total litter N and P were determined by modified micro-Kjeldahl digestion (Parkinson and Allen 1975) and analyzed on a Lachat AE Flow Injection Analyzer (Lachat Instruments, Inc., Loveland, CO, USA), using the salicylate and molybdate-ascorbic acid methods, respectively (Lachat instruments, Inc. 1992). All final chemical values are reported on an oven-dry (70°C) mass basis.

Statistical analyses

For the observational studies, the effects of galling on leaf litter mass remaining and total N and P dynamics were evaluated with analysis of variance (ANOVA), using treatment, site and sampling date (time) as fixed factors for each study separately (Weider and Lang 1982). We considered site and time as fixed effects as we knew from previous studies that the chosen sites were representative of the range of microclimate variation that cottonwood hybrids and *P. betae* experience (Whitham 1989, Martinsen et al. 2001, Schweitzer et al. unpubl.) and that backcross leaf litter decomposes within two years in the field (Schweitzer et al. 2004). Because there were no interaction effects in either year, and we were interested in the mean differences between treatments, decomposition rate constants (k) were not calculated (Weider and Lang 1982).

For the herbivore exclusion experiment, we compared the mass remaining and N and P dynamics (as percentage of original N and P) among treatments using a mixed-model ANOVA with herbivore treatment and sampling date (time) as fixed effects while genotype was considered a random effect. We considered genotype random as we were interested in the generalizable patterns of decay across genotype (Scheiner and Gurevitch 2001). For this experiment, decomposition rate constants (k) were also calculated to assess differences in rate of decomposition using a single negative exponential model. Decomposition rate constants were estimates as the negative slope from the linear regression of the natural logarithm of the fractional mass remaining at each collection date (Schlesinger and Hasey 1981, Weider and Lang 1982, Hart et al. 1992). Paired t-tests were used for each genotype to determine differences in k with herbivore treatment. For all of these studies, the data were square-root transformed when assumptions of normality and homogeneity of variance were not met.

Comparisons of the litter quality parameters for the galled and non-galled litter from the observational studies were made with t-tests within each year. Comparisons of the initial litter quality parameters from the herbivore exclusion experiment were made with paired t-tests as the two litter types were derived from the same tree genotype. In the herbivore exclusion experiment, we also compared the initial litter chemistries to the density of *P. betae* on the branches of each genotype to determine if herbivore density was related to the chemical quality of the leaf litter. Gall density was assessed during the growing season by counting the number of galls on 100 shoots on control branches of each genotype. We also used linear regression to compare the concentration of each chemical response variable (total N, P, condensed tannin and lignin) with the number of galled leaves per branch.

Table 1. Summary of leaf litter quality for galled and non-galled leaf litter for the observational studies. Chemical values are presented as mean percent dry weight, with one standard error in parentheses. Leaf litter categories are the leaf lamina from galled leaf litter and non-galled litter. The 1997 and 1999 values represent the mean values of 7 and 9 trees, respectively. Asterisks indicate significant differences between the leaf lamina of galled litter and non-galled leaf litter ($\alpha = 0.05$).

Source of variation	Galled	Non-galled	t	p
1997				
Condensed tannin	16.08 (0.29)	9.87 (1.27)	22.87	0.003*
Lignin	10.96 (0.31)	12.15 (0.62)	2.94	0.137
Nitrogen	0.83 (0.004)	1.09 (0.04)	22.16	0.003*
Phosphorus	0.09 (0.002)	0.09 (0.004)	0.80	0.41
1999				
Condensed tannin	16.47 (0.96)	8.84 (0.54)	23.40	<0.001*
Lignin	19.85 (0.89)	15.17 (0.76)	22.20	<0.001*
Nitrogen	1.17 (0.03)	0.93 (0.03)	49.62	<0.001*
Phosphorus	0.05 (0.002)	0.07 (0.005)	12.85	0.002*

Results

Observational studies

For both observational studies (1997 and 1999), we found that galled litter was generally lower in quality than non-galled litter (Table 1). Condensed tannin concentrations in leaf litter lamina of galled leaves were 39–47% higher than in non-galled leaf litter in both years of study. Nitrogen concentration in the leaf lamina was also significantly different (~24%), though the direction differed between galled and non-galled leaf litter between years. Lignin and P concentrations in the leaf lamina differed between the two litter types in only one of the two years (1999), where lignin concentration was 23% higher and P concentration was 25% lower in galled than in non-galled leaf litter. On average, the gall tissue had lower concentrations of condensed tannins (74–81% lower), lignin (10–35% lower) and N (16–31% lower) than the lamina of a galled leaf; however, P concentrations in gall tissue were higher (43–62.4% higher) than the leaf lamina (data not shown).

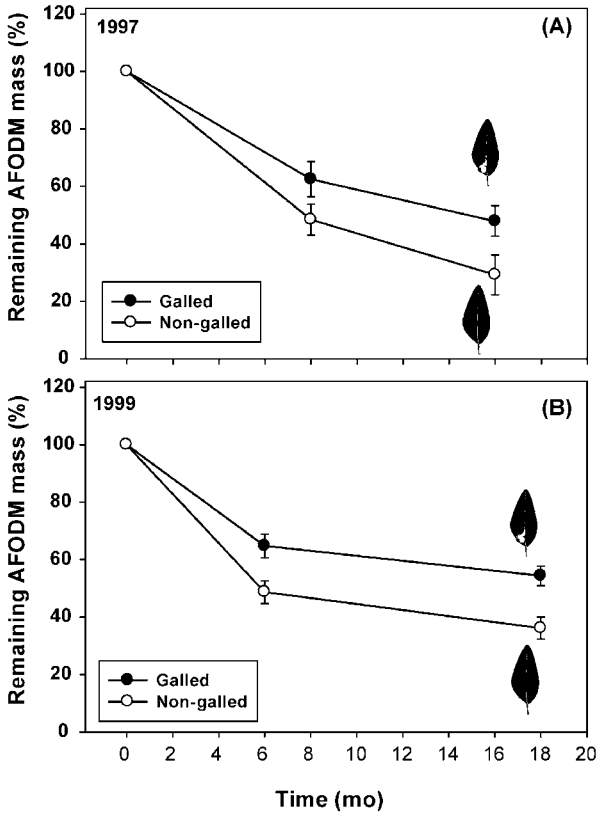

Fig. 1. Decomposition of cottonwood leaf litter at three different sites as influenced by a galling aphid. After 16–18 months of decomposition in the field, galled leaf litter decomposes 34–40% slower than non-galled leaf litter. Each panel represents ash-free oven-dry mass (AFODW) percent mass remaining for naturally galled and non-galled litter from studies begun in 1997 (A) and 1999 (B).

We found that these differences in litter quality translated to differences in leaf litter decomposition for galled and non-galled litter. For both observational studies, we found that galled leaf litter (at the final collection date) decomposed at rates 34 to 40% slower than non-galled leaf litter (Fig. 1). In both years, we found significant herbivore, time and site differences in the amount of remaining leaf litter mass (Table 2).

The overall patterns of N and P during decomposition in each litter type were similar, although the temporal patterns differed between years (Fig. 2). In general, at the end of each study, galled litter exhibited net nutrient release from the litter, while non-galled litter showed net nutrient immobilization. The one exception to this pattern occurred with N in the 1997 study, where both litter types showed similar rates of net N immobilization.

For the 1997 study, we found no site differences or site interactions with the amounts of N and P remaining in the litter, so we removed site as a factor from the ANOVA and re-ran the model with just treatment and time as fixed factors. From this analysis, we found no differences in the amount of N remaining in the litter by treatment ($F = 1.231$, $p = 0.275$) or over time ($F = 1.163$, $p = 0.285$); there also was no interaction between these factors ($F = 3.601$, $p = 0.063$). In contrast, we found that there were significant treatment effects on the amount of P remaining ($F = 58.435$, $p < 0.001$) that did not differ over time ($F = 0.431$, $p = 0.541$) or interact with time ($F = 0.111$, $p = 0.740$). In 1997, overall, P accumulated (i.e. net P immobilization) only in non-galled leaf litter that had lower initial P concentrations (25% lower) than initial galled leaf concentrations.

In the 1999 study, we found that net N and P immobilization occurred only in non-galled litter, but that this effect depended on the degree of decomposition (Fig. 2). There was a significant herbivore treatment effect ($F = 112.19$, $p < 0.001$) on the amount of N remaining, but there was no effect of time ($F = 1.586$, $p = 0.216$); however, we did find a significant treatment by time interaction ($F = 122.38$, $p < 0.001$). The amount of P remaining in the leaf litter showed similar patterns, with a significant herbivore treatment effect ($F = 112.893$, $p < 0.001$) and treatment by time interaction ($F = 101.653$, $p < 0.001$), but no significant main effect of time ($F = 2.009$, $p = 0.165$). For both nutrients and litter types, there was little change in the amount of nutrients present in the leaf litter until after the litter had decomposed for eight months, after which non-galled litter showed net nutrient immobilization while galled litter showed net nutrient release.

Overall, these observational studies suggested that galled litter was more recalcitrant to decomposition, which influenced the rate of mass loss and nutrient dynamics of the litter. These data further suggest that galling influences leaf litter decomposition and nutrient dynamics. However, from these studies alone, we cannot

Table 2. Results from analysis of variance for the observational decomposition experiments (mass remaining) begun in 1997 and 1999. Herbivory refers to whether the leaf litter was galled or non-galled, time refers to the amount of mass remaining at each of two collection dates and site is the amount of mass remaining at each of 2 or 3 field sites.

Source of variation	df	F	p
1997			
Herbivory	1	19.94	<0.001
Time	1	21.24	<0.001
Site	2	9.94	<0.001
Herbivory × time	1	0.40	0.53
Herbivory × site	2	0.09	0.92
Time × site	2	1.95	0.15
Herbivory × time × site	2	1.45	0.25
1999			
Herbivory	1	20.27	<0.001
Time	1	65.14	<0.001
Site	1	0.36	0.55
Herbivory × time	1	2.91	0.09
Herbivory × site	1	0.53	0.47
Time × site	1	0.37	0.55
Herbivory × time × site	1	0.14	0.71

determine if the differences are induced by the aphid or if the aphid stem-mother selects leaves with lower leaf quality. The following experiment discriminated between these alternatives.

Herbivore exclusion: litter chemistry

When we experimentally prevented *P. betae* colonization of susceptible trees, we found similar patterns in litter quality to the observational studies; however, individual tree genotypes exhibited high variation in the patterns of altered leaf chemistry (Fig. 3). Averaged across all ten genotypes, the leaf lamina of galled leaves also exhibited elevated concentrations of secondary compounds and nutrients relative to non-galled leaves, similar to the induced effects found (in at least one of the years) in the observational studies; condensed tannins were 18% higher, lignin was 23% higher, N was 25% higher and P was 46% higher. We also found that the gall tissue had lower concentrations of condensed tannins (61% lower), lignin (23% lower) and N (39% lower) than the leaf lamina, while P concentrations were higher (29%) in the gall tissue (data not shown); these results are consistent with those found in the observational studies. Paired comparisons of leaf litter chemistry between the galled and gall-excluded leaves showed significant differences in the concentrations of litter condensed tannin (paired $t = 1.886$, $p = 0.046$), lignin (paired $t = 4.645$, $p = 0.0005$) and P (paired $t = 2.023$, $p = 0.037$), while there was no significant difference in litter N (paired $t = 1.554$, $p = 0.078$). While litter quality was reduced with herbivory (averaged across all clones), genotype-specific responses to herbivory indicated that these averages do not adequately represent the responses of individual trees to herbivory.

Interestingly, the variation in chemical quality between genotypes does not seem to be related to gall density. We found that gall density regressed against each chemical response variable did not explain much of the variation in litter quality within genotypes. We found no relationship between number of galls on the control branch and leaf-level chemical concentrations of condensed tannins ($r^2 = 0.077$, $p = 0.468$), lignin ($r^2 = 0.0602$, $p = 0.517$), N ($r^2 = 0.056$, $p = 0.539$) or P ($r^2 = 0.171$, $p = 0.268$). These data indicated that the induction response to herbivory is genotype-specific and not necessarily related to the abundance of the herbivore.

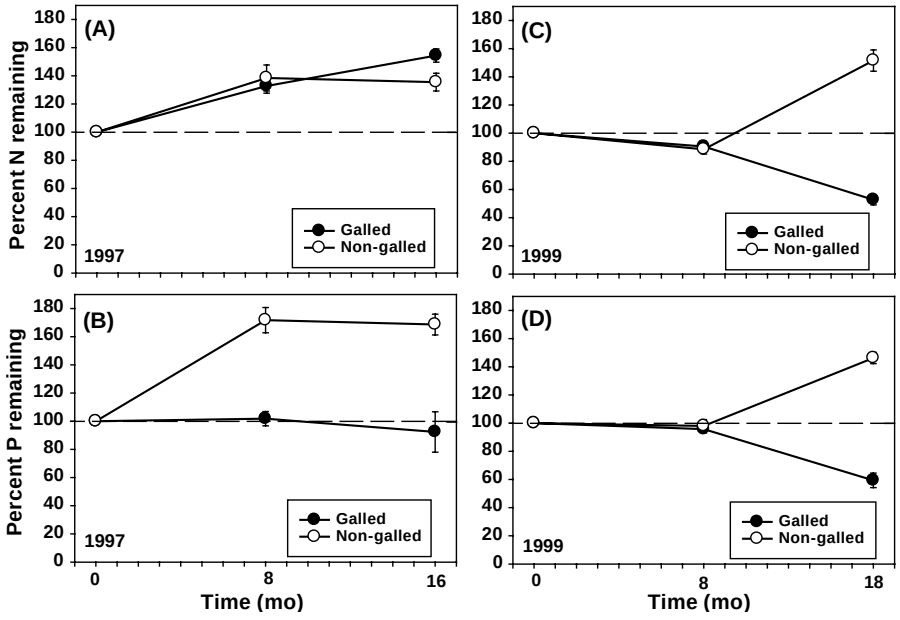

Fig. 2. Nitrogen (N) and phosphorus (P) dynamics during the decomposition of cottonwood leaf litter at three different sites as influenced by a galling aphid. There were significant differences in net N and P immobilization between experiments in 1997 and 1999. During the 1997 study, there was no difference in N dynamics between galled and non-galled leaf litter (A). Phosphorus (B) showed significant net immobilization in non-galled leaf litter relative to galled litter, which exhibited net P release. After 18 months in the 1999 study, net immobilization of both N (C) and P (D) occurred in non-galled leaf litter, while net N and P release occurred in galled leaf litter.

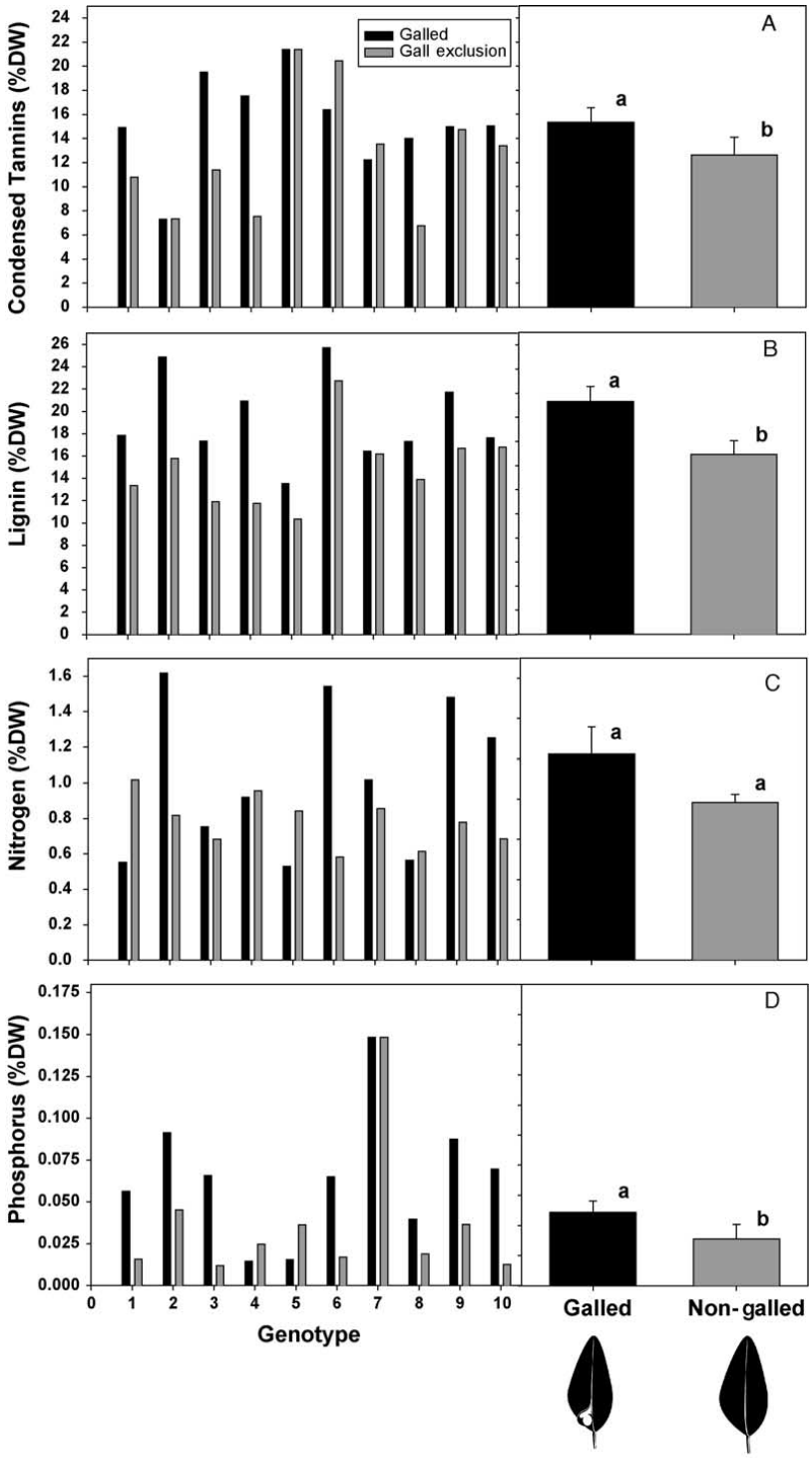

Fig. 3. Left panels: Mean dry-weight concentrations of condensed tannins (A), lignin (B), nitrogen (C) and phosphorus (D) of the ten clones in the *P. betae* exclusion experiment. Right panels: dry-weight concentrations of these same constituents for galled leaf litter and gall excluded leaf litter, averaged across all ten clones.

Herbivore exclusion: litter decomposition and nutrient dynamics

The presence of galls had a significant effect on rate of leaf litter decay. Similar to the observational studies, the galled and gall-excluded litter from the individual genotypes decomposed at different rates. Averaged over all five of the genotypes used in the decomposition study (clones 1–5), we found that galled litter decomposes 18% slower (based on mean decomposition rate constants) than non-galled litter. There were significant herbivore treatment, genotype, and time effects between the main factors (herbivore treatment: $F = 8.19$, $p = 0.035$; genotype: $F = 3.38$, $p = 0.10$; time: $F = 135.65$, $p = < 0.0001$). We found no interactions between time by genotype ($F = 1.06$, $p = 0.46$) or herbivore treatment by time by genotype ($F = 0.70$, $p = 0.78$) however we did find a significant interaction between herbivore treatment by

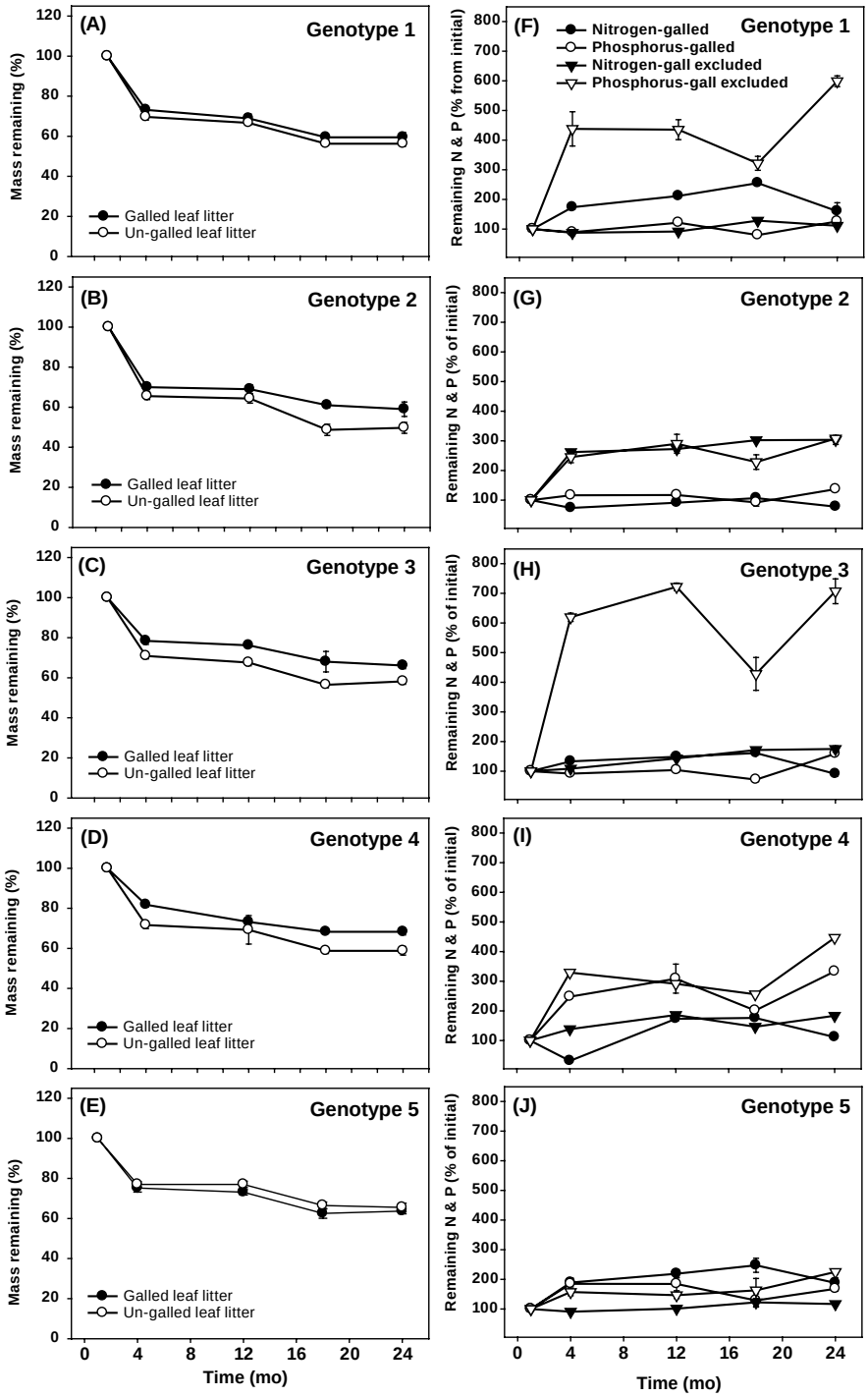

Fig. 4. Cottonwood genotype interacted with herbivore treatment to alter leaf litter decomposition and nutrient dynamics in complex ways. (A)–(E) represent the proportion of mass remaining for each individual clone for each treatment (galled and gall excluded). In all genotypes except for one (clone 5), galled litter decomposed slower than non-galled litter. Each point represents a mean of 5 replicates. Calculated annual decomposition rate constants for each clone are as follows: clone 1 galled litter $k = 0.305$, gall excluded litter $k = 0.381$; clone 2 galled litter $k = 0.317$, gall excluded litter $k = 0.426$; clone 3 galled litter $k = 0.214$, gall excluded litter $k = 0.337$; clone 4 galled litter $k = 0.233$, gall excluded litter $k = 0.301$; clone 5 galled litter $k = 0.279$, gall excluded litter $k = 0.250$;. (F)–(J) represent the percent of the initial nitrogen and phosphorus remaining in the leaf litter during decomposition, for each treatment and clone.

time ($F = 3.69$, $p = 0.03$) and treatment and genotype ($F = 11.40$, $p < 0.0001$), indicating that tree genotype influenced the effect of the herbivore on leaf litter decomposition (Fig. 4A-E). When we made pair-wise comparisons of decomposition rate constants (k), we found that galled leaf litter had a significantly lower decomposition rate constant than gall-excluded leaves for all clones except for clone 5 (clone 1, $t = 5.995$, $p < 0.001$; clone 2, $t = 6.18$, $p = 0.003$; clone 3, $t = 9.555$, $p < 0.001$; clone 4, $t = 13.769$, $p < 0.001$; clone 5, $t = 2.126$, $p = 0.066$). There was similar or greater variation in litter quality and decomposition rates among clones than the variation in these factors caused by herbivory. For example, we found the difference in decomposition rate constants between galled and gall-excluded treatments within a single genotype can vary up

to 30%, while the differences in decomposition rate constants across genotypes (gall excluded) can vary up to 41%.

The measured initial chemical parameters of leaf litter that correlated with decomposition rate differed between herbivore treatments. In gall-excluded litter, we found the concentration of lignin in the initial litter was the best predictor of decomposition rate constants across all genotypes ($F = 13.44$, $r^2 = 0.769$, $p = 0.05$). In the galled litter, the initial concentration of P was the best predictor of decomposition rate constant across all genotypes ($F = 10.0$, $r^2 = 0.817$, $p = 0.035$). Together, these data argue that the mechanisms for the differences in leaf litter decomposition were due to the differential effects of herbivory on leaf litter quality. Specifically, leaves respond to the presence of the gall with induced or altered secondary chemical or nutrient concentrations, which reduces the quality of galled leaf litter and alters decay.

The differences in leaf litter quality and decomposition rate among genotypes and between herbivore treatments extend to the dynamics of nutrients contained within these litters (Fig. 4F-J). We found significant time effects ($F = 14.94$, $p < 0.0001$), herbivore treatment by time ($F = 14.20$, $p < 0.0001$), herbivore treatment by genotype ($F = 167.51$, $p < 0.0001$) and herbivore treatment by genotype by time ($F = 3.23$, $p < 0.0001$) interactions on the change in litter N.

However, there were no significant herbivore treatment ($F = 0.015$, $p = 0.91$), genotype ($F = 0.08$, $p = 0.985$) or genotype by time ($F = 1.33$, $p = 0.32$) effects. Similarly, changes in litter P showed idiosyncratic effects with significant time ($F = 18.14$, $p < 0.0001$), herbivore treatment by genotype ($F = 50.10$, $p < 0.0001$) and herbivore treatment by genotype by time ($F = 3.86$, $p < 0.0001$) effects. There were no significant herbivore treatment ($F = 5.27$, $P = 0.083$), genotype ($F = 0.57$, $p = 0.701$), herbivore treatment by time ($F = 3.13$, $p = 0.07$) or genotype by time ($F = 0.84$, $p = 0.62$) effects. Taken together, these data suggest complex interactions among herbivory, genetically controlled differences in litter quality and the nutrient requirements of the microbial decomposer community during various stages of litter decomposition.

However, if we compare the paired differences in both N and P dynamics between herbivore treatments after 24 months of decomposition in the field, we find significant differences in rates of net nutrient accumulation (i.e. net immobilization) and release for all five genotypes. We found that the N dynamics during litter decomposition of all genotypes differed between herbivore treatments after 24 months in the field (genotype 1: paired $t = 2.62$, $p = 0.03$; genotype 2: paired $t = 22.58$, $p < 0.0001$; genotype 3: paired $t = 22.93$, $p < 0.0001$; genotype 4: paired $t = 21.1$, $p < 0.0001$; genotype 5: paired $t = 5.42$, $p = 0.003$). Specifically, genotypes 2 and 3 had a net release of N relative to gall-excluded leaves after 24 months in the field, while galled litter from genotypes 1 and 4 had greater net N immobilization than the gall excluded litter. Genotype 5 litter experienced net N immobilization in both litter types, but gall-excluded litter had greater amounts of net N immobilization (Fig. 4). Similarly, we found that all five genotypes differed between herbivore treatments in the amount of P remaining after 24 months in the field (genotype 1: paired $t = 42.29$, $p < 0.0001$; genotype 2: paired $t = 34.34$, $p < 0.0001$; genotype 3: paired $t = 23.22$, $p < 0.0001$; genotype 4: paired $t = 3.68$, $p = 0.011$; genotype 5: paired $t = 16.6$, $p < 0.0001$). We found that both herbivore treatments had exhibited net P immobilization by the end of the experiment, however gall-excluded litter for all 5 genotypes accumulated 26–78% greater amounts of P than galled litter.

Discussion

Over a six year period, with two observational studies and an experiment, our results argue that the independent and combined effects of herbivory and plant genotype influence decomposition and nutrient dynamics in three major ways: 1) galling by *P. betae* generally reduced leaf litter quality as well as the rate of litter decomposition; 2) non-galled leaf litter, averaged across all genotypes, accumulated more N and P than galled litter, indicating that the herbivore-induced differences in leaf litter quality can alter decomposer nutrient requirements during leaf litter decay; and 3) variation in plant genotype response to herbivory by galling aphids results in variation in the patterns and rates of decomposition and nutrient release, which may create considerable variation in nutrient flux on the landscape. Because of the magnitude of these effects, in the following sections we contend that both herbivory and genetic variation may have significant impacts on nutrient dynamics in this riparian forest ecosystem.

Herbivores as decelerators of ecosystem-level processes

Studies examining the effects of arthropod herbivores on ecosystem processes commonly find that herbivores accelerate nutrient cycling through a variety of mechanisms (Ritchie et al. 1998, Hunter 2001, Chapman et al. 2003), while examples of arthropod herbivores decelerating nutrient cycling in ecosystems are less common. Herbivore-mediated positive feedbacks could decelerate ecosystem processes by altering leaf/root litter inputs in at least two ways: 1) by decreasing the abundance of nutrient rich or poorly defended plant species (or genotypes) through preferential feeding (Ritchie

et al. 1998, Wardle et al. 2002); and 2) by reducing leaf litter quality within the remaining plant leaves through biochemical induction of secondary compounds and lignin (Schultz and Baldwin 1982, Findlay et al. 1996). Our study found that reductions in leaf litter quality from herbivory by a galling aphid decelerated decomposition by up to 40% (Fig. 1 and 3) and altered leaf litter nutrient dynamics during decomposition (Fig. 4). If herbivore-driven changes in leaf litter chemistry such as this are common, than herbivore-induced litter quality could be an important component affecting nutrient cycling in many ecosystems (Choudhury 1988, Findlay et al. 1996, Hunter 2001).

It is often suggested that herbivore-induced reductions in litter quality, via induction of secondary compounds and lignin, could be an important mechanism for altered nutrient cycling (Schowalter 2000, Hunter 2001). However, we are aware of only a few studies that have experimentally demonstrated such an effect. Findlay et al. (1996) found that both herbivory and exposure to ozone can alter the polyphenol content of living leaves that were retained with leaf senescence, and slowed rates of decomposition. Furthermore, Grime et al. (1996) experimentally demonstrated a positive correlation between herbivore palatability and rate of decomposition that supports the premise that plant defenses may link community patterns and ecosystem properties.

Gall-forming arthropods may be especially good at altering host plant litter quality due to herbivore-induced hypersensitive responses during the formation of the gall. Galls often act as mobilizing sinks for plant resources (Larson and Whitham 1991, Hartley 1998, Fernandes and Negreiros 2001, Arnold and Schultz 2002); they have been found to alter leaf secondary chemistry in either the gall tissue or surrounding leaf lamina, presumably to protect the developing offspring from parasite and fungal attack (Taper and Case 1987, Weis et al. 1988, Abrahamson et al. 1991, Hartley 1998, Nyman and Julkunen-Titto 2000). Our data support previous work in which the leaf lamina of a galled leaf contained higher concentrations of polyphenols and lignin than the gall tissue itself (Hartley 1998). However, this pattern is often dependent on the species of both the plant and gall-former, and the opposite effect has also been reported. Regardless, we are aware of no previous studies that have examined the effects of gall-induced compounds on leaf litter quality after leaf senescence or on the subsequent rate of decomposition, even though galling insects are common and found world-wide (Price et al. 1998). The generally higher concentrations of condensed tannin, lignin and P (and sometimes N) in the lamina of galled leaves result in lower rates of litter decomposition and alterations in nutrient release that may have important effects on ecosystem N and P cycling. Furthermore, we found that the induced changes in litter quality were unrelated to herbivore density, which argues that galling aphids have a unique effect on C allocation patterns that is density independent. Manipulation of gall density within a leaf has been shown to result in altered C and N allocation (Larson and Whitham 1991, Hartley 1998), but we are unaware of any studies relating gall density within a branch or tree to leaf or litter chemistry.

Genetic effects

Both plant genetic variation and herbivory of plants are two factors that together could have large and predictable effects on ecosystem processes, but are often not considered in ecosystem assessments. Studies examining the effects of biodiversity on ecosystem processes commonly focus on species variation, and have found idiosyncratic relationships between species diversity and ecosystem processes such as productivity and nutrient cycling (Tilman et al. 1997, Loreau et al. 2001, Naeem 2001). The genotype-specific responses we observed with herbivory (Fig. 3 and 4) argue that finer scales of analysis may be required to gain understanding of processes such as nutrient cycling. This is emphasized by our findings that the differences in decomposition between genotypes may be as large as differences between plant species (e.g. such as pine and oak; Bockheim et al. 1991).

Feedbacks between plant genotype, resistance and susceptibility to herbivores, and leaf/litter chemistry could result in very different patterns of nutrient cycling at local scales. Plant species (Kleb and Wilson 1997), mammalian herbivores (Pastor et al. 1998, Burke et al. 1999) and disturbance (Robertson et al. 1993) have all been shown to effect spatial variation in soil nutrient availability. For example, a recent study by Augustine and Frank (2001) found that grazing herbivores have substantial effects on the distribution of soil N from the individual plant to the landscape scale, via changes in the plant community and plant litter inputs. However, to date, the effects of plant genotype or arthropod herbivores on nutrient heterogeneity across a landscape has not been documented experimentally (Stark 1994). Genotype-mediated insect alterations of litter inputs and quality, such as demonstrated with our study, suggest a similar pattern may also occur in this (and other) ecosystems with a dominant arthropod herbivore. Since most forest ecosystems are not composed of a single genotype, the variation that genotype-specific responses may introduce on ecosystem-level processes is worthy of further investigation, and could have important implications for linking above- and below-ground processes at fine spatial scales (Bardgett et al. 1998, Hooper et al. 2000, Bardgett and Wardle 2003).

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