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NONADDITIVE EFFECTS OF MIXING COTTONWOOD GENOTYPES ON LITTER DECOMPOSITION AND NUTRIENT DYNAMICS

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Abstract. Plant species litter mixtures often result in nonadditive differences in ecosystem processes when compared to the average of their individual components. However, these studies are just beginning to be extended to the genotype level and to our knowledge have not incorporated the effects of herbivory or genotype-by-herbivore interactions. With a two-year field study, using genotypes that differed by as few as three restriction length polymorphism (RFLP) molecular markers, we found three major patterns when we mixed leaf litters from different genotypes both with and without previous herbivory. First, leaf litter genotype mixtures, regardless of herbivory, demonstrated nonadditive rates of decomposition and nutrient flux. Second, mixed genotype litter without herbivory decomposed faster than the same genotypes with herbivory. Third, in genotype mixtures, with and without herbivory, we found that net rates of immobilization of both nitrogen and phosphorus can differ from expected values (based on genotype means) by as much as 57%. These results show that mixing litter genotypes can alter rates of decay and nutrient flux and that the effects are reduced with herbivory. Nonadditive effects at the genotype level that we report here are nearly as large as what has been recorded for plant species mixtures and may have important, though under-appreciated, roles in ecosystems. These data further suggest that genetic diversity and genotype-by-herbivore interactions can affect fundamental ecosystem processes such as litter decomposition and nutrient flux.

Key words: *condensed tannins; herbivory; induced resistance; leaf litter decomposition; mixing litter; nonadditive effects; plant genotype;* Populus.

INTRODUCTION

Most studies of decomposition processes have used plant leaf litter from single species; however, most terrestrial ecosystems consist of a mixture of plant species and the leaf litters they produce intermingle during decomposition. Litter interactions during decomposition may alter decomposition rates and nutrient dynamics during decay from what might be expected from single-species studies. In a recent review, Gartner and Cardon (2004) showed that such nonadditive effects (synergistic if enhanced in mixtures and antagonistic if reduced in mixture) are common. However, even plant monocultures consist of many different plant genotypes whose litter also decomposes in mixtures in the field, and the possible effects of intraspecific variation in plant litter on decomposition processes is just beginning to be assessed (Madritch and Hunter 2002, 2005). Here, we explore the effects of mixing leaf litters from different plant genotypes and herbivory on these processes.

Herbivory during the growing season can have ''afterlife'' effects on leaves following senescence that may alter rates of leaf litter decay (Choudhury 1988, Findlay et al. 1996, Hunter 2001, Bardgett and Wardle 2003, Schweitzer et al. 2005), and these effects could result in nonadditive outcomes when litter decomposes in mixtures. For example, herbivory on green leaves can alter translocation of nutrients before senescence, leading to leaf litter with higher nitrogen (N) concentrations (Cobb and Orwig 2002, Chapman et al. 2003). Herbivores may also induce secondary compounds such as tannins that are retained with senescence and slow rates of litter decay (Findlay et al. 1996, Schweitzer et al. 2005). Thus, in addition to the innate differences in plant chemistry among genotypes, there is a second level of complexity in the plant genotype-by-herbivore interaction that may also affect decomposi-

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tion in litter mixtures. Differences in leaf litter secondary chemistry and mineral content (whether constitutive or induced by herbivory) can decelerate or accelerate rates of decay and nutrient release by changing the recalcitrance or palatability of litter to decomposers (Horner et al. 1988, Grime et al. 1996). As plants can be quite variable in their resistance and susceptibility to herbivores (Whitham 1983, Strauss et al. 2004), mixtures of leaf litters with herbivory are likely to be common, although we are unaware of any studies that have assessed if mixing of herbivore-altered leaf litters results in nonadditive effects during decomposition.

In a previous study we demonstrated that litter from genotypes decomposed separately, with or without previous herbivory, can have different rates of litter decomposition and nutrient dynamics (Schweitzer et al. 2005). Here we describe the results of a separate, companion experiment in which we mixed litter from five genotypes with and without herbivory to address the following questions: (1) Does mixing of litter from different tree genotypes result in altered rates of decomposition and nutrient flux relative to what would be expected from the patterns observed from the genotypes decomposed individually? (2) Does mixing of litter from genotypes that have experienced previous herbivory result in altered rates of decomposition and nutrient flux relative to what would be expected?

Materials and Methods

As a separate experiment from a companion study (Schweitzer et al. 2005), we quantified rates of leaf litter decomposition and nutrient flux for mixtures of five *Populus* genotypes (Salicaceae) that had experienced herbivory during the growing season, compared to control leaf litter in which herbivores were excluded. *Pemphigus betae* (Aphididae, Homoptera) is a petiole gall-forming aphid that commonly occurs on backcross hybrids (*Populus fremontii* S. Watson × *P. angustifolia* James) throughout the western United States. Aphid-susceptible trees were recognized at a single site in the field within a naturally occurring *Populus* hybrid swarm along the Weber River in northern Utah, USA (41.2° N, 112.0° W). The trees were identified as individual genotypes with restriction length polymorphism (RFLP) analyses, differed by three or fewer molecular markers (Martinsen et al. 2001), and have distinct genetic-based leaf chemistries (Whitham et al. 2003). In spring 2000 we performed an herbivore exclusion experiment on paired branches of individual backcross genotypes by placing a sticky barrier on branches to prevent colonization by aphid stem-mothers (see exclusion details in Schweitzer et al. [2005]) and collected the leaf litter (galled and gall-excluded from the same genotype) in 2 mm diameter mesh bags after senescence in the fall.

Decomposition litter bags (10 × 15 cm) were constructed of polyester mesh with 3-mm openings on the top and 0.5-mm openings on the bottom. We placed equal proportions of air-dried, galled and gall-excluded litter for each of five genotypes in separate litter bags to examine the effects of mixing genotype litters. The mixed litter bags had similar total initial mass as individual genotype litter bags (i.e., 3–5 g, which is comparable to field rates of litterfall [Schweitzer et al. 2004]). This design resulted in separate litter bags that had mixtures of all five genotypes with galls and mixtures of all five genotypes with the gall-excluded litter and no other obvious herbivore damage by other arthropod species. We made five litter bags for each of four collection dates, collected after 2, 6, 12, and 24 months in the field (a mixture of all five genotypes × two herbivore treatments [galled or gall-excluded] × five blocks × four collection dates). Litter bags were randomly assigned to five blocks (composed of all genotype treatments and collection dates in random order) that were placed in random locations under the tree canopies on the surface of the forest floor at the same site where the litter was collected. The litter bags were attached to the forest floor during the time of maximum litterfall (October 2000) with steel nails and left to decompose. At each collection date the litter bags were transported back to the laboratory on ice where all contaminants were removed; the samples were then air-dried in paper sacks, weighed, and ground (<425 μm) with a Wiley mill and stored in a −80°C freezer until chemical analyses were performed. All final masses are expressed on an ash-free (500°C for 1 hour), oven-dry (105°C for 48 hours) mass basis.

Initial litter chemistry of ground subsamples (condensed tannin, lignin, nitrogen, and phosphorus) was quantified for each individual genotype (with and without herbivory), as well as for a mixture of all genotypes in equal proportion by mass to determine if mixing litters resulted in a different overall chemical quality of the litter. Total N and phosphorus (P) were also calculated at each collection date to determine differences in net nutrient immobilization and release, relative to the initial amount of these elements present in the litter bag (i.e., as percentage of original N and P). Condensed tannins were determined by the butanol-HCl method (Porter et al. 1986), lignin was determined with the acetyl-bromide method (Ilyama and Wallis 1990), and total N and P were determined by modified micro-Kjeldahl digestion (Parkinson and Allen 1975). Details for all chemical analyses are described in Schweitzer et al. (2005).

Statistical analyses

To assess if nonadditive effects occurred in rates of litter decay when the galled and gall-excluded genotypes were mixed, we compared expected decomposition rate constants (based on the individual genotype decomposition constants) to the observed decomposition constants of galled and gall-excluded litter in the mixed genotype litter bags. After confirming normality and homogeneity of variances, we compared the observed vs. the expected decomposition rate constants with a paired *t* test across blocks. Decomposition rate constants were estimates based on the negative slope from the linear regression of the natural logarithm of the fractional ash-free dry mass remaining at each collection date for each individual genotype and the genotype mixture (Weider and Lang 1982). Expected decomposition rate constants were calculated within a block using the following method (Blair et al. 1990, Wardle et al. 1997):

$$k_e = (G1_1 + G2_1 + G3_1 + G4_1 + G5_1)/5$$

where the expected litter decomposition rate constant (k_e) is calculated by summing the rate constants of the genotype litter decomposed in monoculture of genotypes 1–5 in each block (e.g., $G1_1 + G2_1 + G3_1 + G4_1 + G5_1$), divided by the total number of genotypes ($n = 5$ blocks total). Expected total N and P loss after 24 months in genotype mixtures were calculated in the same manner as the expected decomposition rate constants at each collection date.

We compared individual genotype litter chemistry values to the concentrations of the genotypes in mixture with a one-sample *t* test, with the mixed genotype mean as the test value. We also compared the final observed and expected N and P contents of the litter bags at the last collection date (24 months) with a paired *t* test to determine the net differences (accumulation or loss) in N and P of the mixed litter to expected values from individual genotypes after two years of decomposition in the field.

RESULTS

We found that mixing genotypes with and without herbivory both resulted in nonadditive outcomes in litter decomposition, as well as N and P flux, relative to what was expected based on the individual genotype means. After 24 months in the field, total mass loss was 8% faster than expected for genotypes with herbivore damage in mixture, as compared to 16% faster than expected for genotypes without herbivore damage in mixture (data not shown). When we compared the decomposition rate constants (a holistic exponential model of decay over all collection dates [Schlesinger and Hasey 1981]) of the mixed litter bags, with and without herbivory, with the expected decomposition rate (k_e), we found that having mixtures of genotypes in the same litter bag resulted in synergistic effects (i.e., nonadditive effects enhanced from the mean of their individual effects) on leaf litter decomposition (Fig. 1). The mean decomposition rate constant of the mixed genotype, gall-excluded litter bags (i.e., observed rates) was ~12% higher than k_e (i.e., expected rates; paired $t = 3.88$, $P = 0.009$). Similarly, decomposition rate constants of galled genotype mixtures were ~9% higher than would be predicted based on the galled genotype averages (k_e; paired $t = 4.10$, $P = 0.008$). Overall, galled litter decomposition rate constants were lower (i.e., they decomposed more slowly) than nongalled litter treatments.

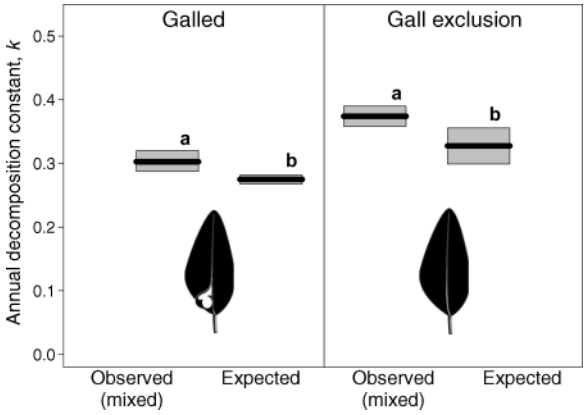

FIG. 1. Decomposition rates (*k*) of galled and gall-excluded mixed litter bag samples; both decay faster than would be expected based on the average of the individual genotypes decomposed separately. Each plot represents the observed and expected mean decomposition rate constant (black line) surrounded by the standard error of the mean (± SE). Herbivory results in an ~19% decrease in the decomposition rate constant, whether decomposed in a mixture of genotypes or single genotypes. Expected values are the blocked means of the individual genotypes' decomposition rate constants. Different letters within each treatment indicate significant differences between the observed and expected values ($\alpha = 0.05$).

Overall, decomposing litter in genotype mixtures resulted in faster rates of nutrient release (or reduced net immobilization) after two years in the field than what would be expected based on the individual genotypes. We found that patterns of N and P net immobilization and release from litter were affected by the mixtures of genotypes but were reduced by herbivory (Fig. 2). For both N and P, we found that mixing genotypes in the same litter bag results in reduced net immobilization of these nutrients than would be predicted based on the individual-genotype average. For example, we found after two years of decomposition that there was a 10 and 57% difference in gall-excluded litter N and P content, respectively, than would be predicted from

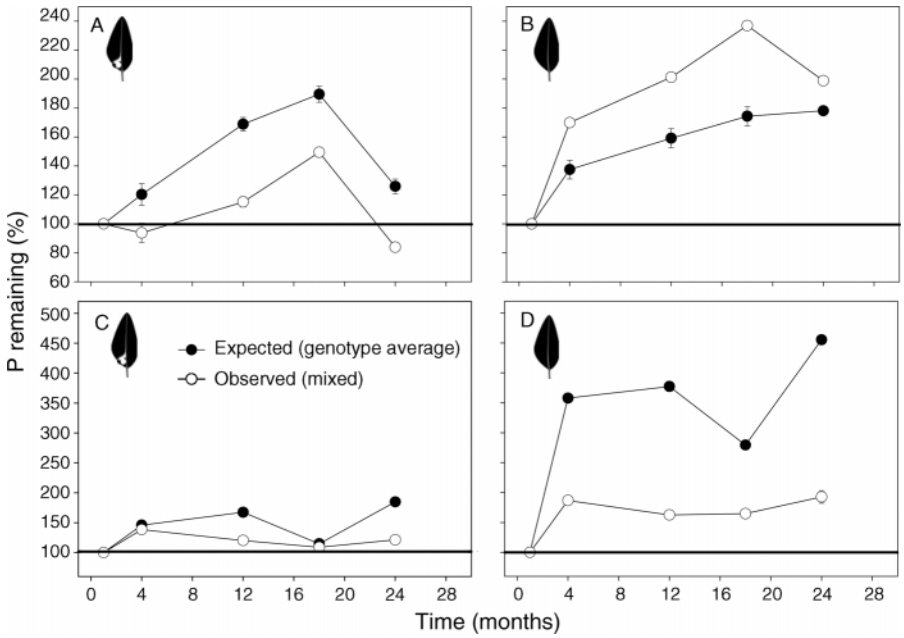

FIG. 2. Nitrogen (A and B) and phosphorus (C and D) dynamics in galled and gall-excluded litter decomposing in the field based on expected (genotype averages) and observed (mixed litter bags) values. Expected values (solid circles) are the blocked means of the individual genotypes. Values above 100% indicate microbial immobilization; after 24 months there is little net release of N or P.

the individual genotypes. Similarly, with herbivory we found that galled litter in mixture accumulated N and P about 33 and 34% slower, respectively, than would have been expected from the individual genotypes. Both galled and gall-excluded litter in mixture differed significantly in N from what was expected from the individual genotypes (galled: paired $t = 7.07$, $P = 0.001$, gall-excluded: paired $t = 7.45$, $P = 0.01$). However, there was net N release from galled mixtures after 24 months (Fig. 2A), while gall-excluded litter had the reverse pattern and accumulated more N than expected (Fig. 2B). We found that both galled and nongalled litter in mixture lost less P than expected based on the individual genotypes (galled: paired $t = 59.1$, $P < 0.001$, gall-excluded: paired $t = 15.6$, $P < 0.001$). There was no net loss of P in either galled or gall-excluded litter mixtures (Fig. 2C, D); in both of these treatments net P immobilization occurred.

As a potential explanation for these patterns, we examined whether the litter chemistry of genotypes in mixture varied from the initial litter quality of the individual genotypes. Overall, we found that mixing litter from multiple genotypes predictably resulted in an average chemical ''signature'' that was representative of the mean of the individual genotypes that made up the mixture (Fig. 3). The initial litter chemistry of galled leaf litter from individual genotypes was similar to that of the genotype mixtures for condensed tannins ($t = 0.20$, $P = 0.43$), N ($t = -1.48$, $P = 0.17$), P ($t = -1.37$, $P = 0.12$) or lignin ($t = 1.95$, $P = 0.62$). Likewise the gall-excluded leaf litter from individual genotypes did not differ from the mixture of genotypes for condensed tannins ($t = -0.03$, $P = 0.47$), nitrogen ($t = 1.27$, $P = 0.15$), P ($t = 0.68$, $P = 0.26$) or lignin ($t = -0.94$, $P = 0.20$). Importantly, this result eliminates an alternative explanation for the patterns and suggests that the differences that we observed in decomposition and nutrient flux were not based on overall differences in litter quality of the mixed genotype treatments, but may instead be associated with greater niche diversity for the decomposer community.

DISCUSSION

This study demonstrates that changes in decomposition rates and nutrient fluxes during decomposition in genotype litter mixtures (compared to expected rates based on the patterns of individual genotypes that comprise the mixtures) are nearly as large as differences observed previously at the plant species level. Mixed plant species (interspecific) litter decomposition experiments have commonly found synergistic outcomes relative to expected decay rates (Gartner and Cardon 2004 and references therein). Many of the mixed species litter studies to date demonstrate accelerated mass loss by the end of the study period (~20 to 65%) relative to single-species litters (Gartner and Cardon

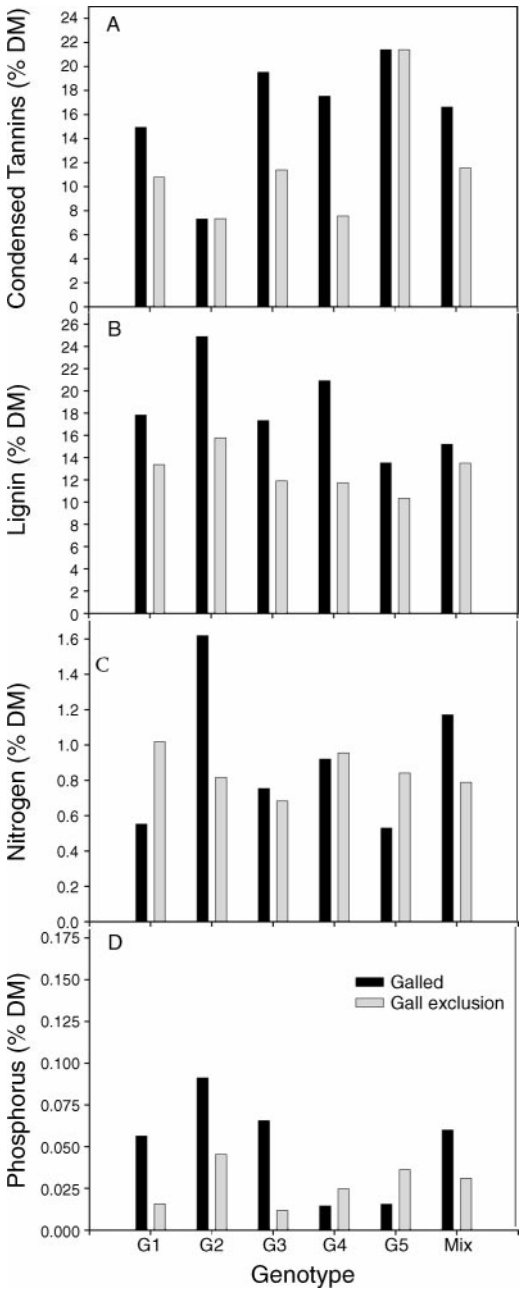

FIG. 3. Litter chemistry of five individual genotypes (G1–G5) alone and in a mixture, with and without galls. The individual genotypes differ substantially in initial litter chemistry, but initial chemical analyses of litter mixtures of all genotypes (with and without aphid galls) are similar to the calculated mean of the individual genotypes. Results are presented as percentage dry mass for genotype leaf litter: (A) condensed tannins, (B) lignin, (C) nitrogen, and (D) phosphorus, for both galled leaves (leaf blade only, black bars) and gall-excluded treatments (gray bars). The figure is from Schweitzer et al. (2005), with substantial modifications.

2004). Here, we surprisingly found that genotypes in mixtures (without herbivory) can vary 16% in mass loss at the end of the experiment (i.e., at the final collection date after 24 months). When we calculate decomposition rate constants (an exponential index of decay that incorporates decay dynamics over all collection dates, not just at the end of the experiment [Schlesinger and Hasey 1981]) we found that decomposition rate constants of litters in mixture can differ by ~12%. Similarly, with nutrient dynamics, mixed species litter decomposition studies commonly find nonadditive nutrient flux patterns at the end of the experiment, relative to what would be expected from single species alone. In this study, after 24 months in the field, we found that nutrient release and immobilization in genotype mixtures can differ by as much as 57%, supporting the idea that genotypes in mixtures can vary as much as plant species from expected rates. Furthermore, as in other broad-leaf studies at the species level, we found that mixing genotype litters resulted in reduced immobilization of N and P (Blair et al. 1990, Briones and Ineson 1996). We are aware of only a handful of studies demonstrating similar effects at a scale finer than species (i.e., phenotype). For example, Madritch and Hunter (2002, 2005) found that nine phenotypes of oak litter in mixture significantly differed in rates of decomposition relative to litter amendments of individual phenotypes alone. They also found that the soils underneath these litter amendments had contrasting soil N availability, total carbon, pH, and microbial biomass content. While species mixtures can have substantial differences in litter quality that create nonadditive effects on ecosystem processes, individual plant genotypes (and phenotypes), such as demonstrated in this study, may commonly exhibit differences just as large.

Mixing genotype litters that experienced herbivory during the growing season also resulted in enhanced rates of decay, relative to the genotypes alone, suggesting that ''afterlife'' effects in genotype mixtures may also alter nutrient dynamics during litter decay. Herbivory during the growing season overall reduced the difference in observed vs. expected rates of litter decay (and nutrient flux) after senescence. This result demonstrates that herbivory can have measurable effects on nutrient dynamics that are rarely factored into decomposition models. As most forest ecosystems are composed of multiple genotypes that vary in their resistance and susceptibility to herbivory, mixtures of leaf litters with and without herbivory are surely common. Our study is unique in that it experimentally examined the effects of mixing litters with previous herbivore damage, and suggests that much more study is required to understand the role of herbivore-induced ''afterlife'' effects on forest nutrient dynamics.

Potential mechanisms for nonadditive effects on decomposition and nutrient flux at the genotype level are likely similar to those operating at the species level. For example, the leaching of nutrients or inhibitory secondary compounds from one litter type to another (Briones and Ineson 1996) may homogenize litter quality. A second, not mutually exclusive, mechanism is that increased niche space occurs in mixtures, which results in higher decomposer diversity, activity, and possibly efficiency (Wardle and Nicholson 1996, Hansen 2000). While we did not examine the litter chemistry of the individual genotype components in the mixed litter bags during decomposition, as they were morphologically indistinguishable, the variability in condensed tannins, N, and P among the five individual genotypes indicates that differences in leaching of litter chemical constituents among the individual genotypes were possible. Homogenization of litter quality could have resulted in the enhanced decay and nutrient dynamics that we observed if decomposer activities were also homogenized. Similarly, the generally reduced immobilization when litter was decomposed in mixtures of genotypes than when litter was decomposed individually by genotype, for both galled and gall-excluded litter (with the exception of N in gall-excluded litter), indicates that the synergistic patterns of decomposition were based on differential colonization and utilization by the microbial community. Recent studies have documented enhanced microarthropod (Hansen 2000, Madritch and Hunter 2005) and microbial community diversity with increases in leaf litter diversity (i.e., differences among plant species [Saetre and Bååth 2000, Priha et al. 2001, Sinsabaugh et al. 2002]). The pattern of enhanced decomposition at the genotype level (this study) and at the phenotype level (Madritch and Hunter 2005) suggests that decomposers may also be able to discriminate between differences in substrate quality at even finer scales.

The data reported here have consequences for understanding how genetic diversity and genotype-by-herbivore interactions can affect fundamental ecosystem processes such as litter decomposition and nutrient flux. Importantly, the magnitudes of these effects are nearly as great as those observed among plant species. Four major implications emerge from these findings. First, the nonadditive effects that occur with mixing individual plant genotypes indicate that examinations at the genotype level, as well as incorporation of more interacting factors such as herbivory, are critical next steps to understanding and predicting how biodiversity can alter ecosystem processes. Research at the genotype level may aid in understanding the idiosyncratic results that often occur with mixed species litter decomposition studies (Wardle and Nicholson 1996, Wardle et al. 1997, Nilsson et al. 1999, King et al. 2002). Second, these findings have important evolutionary connotations. Specifically, our findings suggest that a mix of genotypes may affect nutrient cycling, which could positively or negatively affect the ability of an individual tree genotype to take up nutrients within a stand. Thus, the relative fitness of an individual may be dependent, in part, on its community context (Agrawal et al. 2001, Donohue 2003). Third, along with a few other recent studies of the importance of genetic variation at the ecosystem level (Madritch and Hunter 2002, 2005, Fischer et al. 2004, Schweitzer et al. 2004), our findings continue to explore the validity of a genetic approach to ecosystems sciences, which may ultimately place the field within an evolutionary framework. And last, this study highlights the importance of incorporating both genotype and herbivory (and the mixing of these litters) into global decomposition models. Studies in which genotypes within a species are mixed (a hidden treatment) could possibly result in an overestimate of decay and nutrient flux that could skew our understanding of nutrient dynamics in terrestrial ecosystems. Likewise, excluding herbivore-altered litterfall could also seriously over- or underestimate decay and nutrient flux. Taken together, these data suggest that plant genotype and the ''afterlife'' effects of herbivory may have important and measurable effects on ecosystem nutrient pools that warrant further investigation.

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