

Canopy herbivory can mediate the influence of plant genotype on soil processes through frass deposition

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Abstract

The ecosystem consequences of intraspecific genetic variation is an emerging field of research that strengthens the link between population and ecosystem ecology. Despite recent advances, it remains unclear under what conditions (abiotic and biotic) plant genetic variation will be important to belowground processes. Forest canopy herbivores can have large influences on soil processes by altering the timing, quantity, and quality of forest floor inputs. We demonstrate that the frass inputs from canopy folivores (forest tent caterpillars and gypsy moths) reflect the intraspecific variation in green leaf chemistry (C:N, condensed tannins) of the aspen clones on which they fed. We then varied the genotype and nutrient availability of aspen and monitored the decomposition of both gypsy moth frass and senesced leaf litter in laboratory microcosms for 63 days. Aspen genotype influenced the short-term, frass-induced soil respiration as well as the longer-term, litter-induced respiration. In addition, aspen genotype interacted with nutrient availability to influence the activity of extracellular enzymes measured at the end of the experiment. These results suggest that in aspen forests, canopy herbivores can mediate the influence of intraspecific variation on ecosystem processes through frass deposition. Intraspecific variation is likely more important to ecosystem functioning than previously thought when trophic interactions are also taken into account. The potential for genetic variation within a single plant species to influence the ecosystem effects of herbivores highlights the importance of understanding how and when genetic variation matters to ecosystem processes.

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1. Introduction

Herbivores play important roles in forest ecosystems, influencing plant communities (Mulder et al., 1999; Wardle et al., 2002; Fine et al., 2004) and nutrient cycling both above- and belowground (Pastor and Cohen, 1997; Belovsky and Slade, 2000; Wardle et al., 2002). Although herbivore influences on belowground nutrient cycling have been of considerable interest for decades (Schowalter et al., 1986, 1991; Hunter, 2001), the extent and variability of these impacts remain unclear (Lovett et al., 2002; Bardgett and Wardle, 2003).

Forest herbivores can significantly alter the timing and quality of aboveground inputs to belowground processes (Hunter, 2001; Hartley and Jones, 2004). Even at endemic

levels, forest canopy herbivores can have important influences on soil nutrient cycling (Hunter et al., 2003; Stadler et al., 2004; Throop and Lerdau, 2004). For example, during a moderate outbreak of folivores in the southeastern Appalachians, Reynolds et al. (2000) found a three-fold increase in frass, a five-fold increase in soil nitrate availability, and a doubling of stream nitrate exports. These effects are magnified at outbreak levels when complete defoliation can severely alter soil water relations, nutrient cycles, and microbial activity (Lovett and Ruesink, 1995).

Frass deposition is an important, direct mechanism through which canopy herbivores influence belowground processes (Hunter, 2001; Hartley and Jones, 2004; Stadler et al., 2004). Insect frass contains high amounts of nitrogen and is comprised mainly of labile organic material that decomposes quickly (Lovett and Ruesink, 1995), in contrast to the more recalcitrant leaf litter that senesces

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in non-outbreak years. Coprophagous soil arthropods can further increase nutrient release from insect frass and increase soil microbial activity (Zimmer and Topp, 2002). Perturbations to the nitrogen cycle are especially severe because herbivores defoliate leaves before plants resorb nitrogen, as they would under non-outbreak conditions (Lovett et al., 2002). Consequently, herbivores can double the amount of nitrogen transferred from the forest canopy to the soil when compared with leaf litter alone (Hollinger, 1986). Frass is typically thought to increase labile nitrogen inputs, contributing to nitrogen (N) leaching (Swank et al., 1981; Reynolds et al., 2000; Frost and Hunter, 2004). However, in some systems, labile carbon (C) provided by insect frass allows for microbial uptake of N, resulting in decreased N availability for plant uptake (Lovett et al., 2002).

Variation in plant phenotype can have multiple ecosystem level consequences (Whitham et al., 2003). In particular, the chemical variation within a dominant forest canopy species can potentially influence soil processes. Intraspecific variation in secondary metabolites (such as tannins and other phenolics) has been shown to influence leaf litter decomposition and belowground nutrient cycling (Madritch and Hunter, 2002; Madritch et al., 2006). While simple phenolics are often quickly leached from leaf litter and increase soil respiration by acting as carbon substrates, tannins are typically attributed with retarding litter decomposition and soil microbial activity (Horner et al., 1988; Schimel et al., 1996, 1998; Harborne, 1997; Fierer et al., 2001). Variation in secondary metabolites can also influence the distribution of canopy herbivores (Schultz, 1983; Donaldson and Lindroth, 2006), which may result in spatial variation in both the quantity of herbivore-derived frass and the resulting belowground impacts. The *quality* of herbivore-derived frass is also likely to vary according to canopy chemistry. At outbreak levels common to the native forest tent caterpillar (FTC) and introduced gypsy moth (GM), defoliation is often complete regardless of leaf chemistry (Mattson et al., 1991; Donaldson, 2005). The intraspecific chemical variation inherent in green leaves may remain important to soil processes in outbreak years, as frass likely reflects the chemical composition of consumed leaf material.

Plant phenotype determines the ecological role of a species and is controlled by both genotype and the environment. Consequently, investigating the responses of different genotypes in different environments is essential for understanding the relative importance of genotype, environment, and their interactions ($G \times E$) to ecosystem functioning. Here we present the results of experiments designed to investigate: (1) the interactive effects of tree genotype and nutrient availability on insect frass quality, and (2) the effects of host-mediated variation in frass quality on soil microbial activity. Using trembling aspen and GMs as our model system, we compare the microbial activities associated with frass and leaf litter decomposition as influenced by tree genotype and nutrient availability.

2. Methods

2.1. System description

Trembling aspen (*Populus tremuloides*) is the most widespread native tree in North America and among the most genetically diverse known to science (Mitton and Grant, 1996). It is a primary food source for the native FTC (*Malacosoma disstria* Hubner) and the introduced GM (*Lymantria dispar* L.). Populations of both folivores can vary widely among years, with widespread and often complete canopy defoliation of susceptible host species in outbreak years.

The five aspen genotypes used in this study were originally collected from south-central Wisconsin: Dan1 & Dan2 (Dane County, WI), Wau1 & Wau2 (Waushara County, WI), and Sau3 (Sauk County, WI). All five have been identified as distinct genotypes by microsatellite markers. Of 16 loci evaluated, each genotype contained at least four, and up to eight, unique alleles (Cole, 2005).

2.2. Leaf, litter, and frass collection

Foliage for both herbivore species was provided by three-year-old saplings generated via micropropagation techniques (Sellmer et al., 1989; Donaldson and Lindroth, 2006). In 2001, trees were grown in 51 pots containing a 60:40 mix of torpedo sand and silt-loam field soil. All trees received 4.5 g l^{-1} 14–14–14 (N–P–K + micronutrients) Osmocote[®] 3–4 month slow release fertilizer (Scotts Company, Marysville, Ohio) in 2001 (year 1). In 2002, trees were transferred to 401 pots containing a 70:30 mix of torpedo sand and silt-loam soil and nutrient treatments were initiated. Trees in the low-nutrient treatment received 0.5 g l^{-1} 18–6–12 (N–P–K + micronutrients) Osmocote[®] 8–9 month slow release fertilizer, while trees in the high-nutrient treatment received 4.5 g l^{-1} (Hemming and Lindroth, 1995; Osier and Lindroth, 2001). In spring 2003, fertilizer treatments were repeated except that low-nutrient trees received no fertilizer. For each genotype and nutrient treatment, four replicate trees were allocated to insect feeding trials, while three replicate trees were allocated to fall leaf senescence collection. Green leaf chemistry samples were collected from the set of trees used for insect feeding in the spring of 2003, after leaf expansion and immediately before herbivory treatments. Leaf samples were flash frozen in liquid nitrogen, freeze-dried, and stored at -15°C . Naturally senesced leaf litter was collected in the fall of 2003 in 1 cm^2 mesh netting. Netting was emptied throughout leaf senescence to prevent leaching by intermittent rains. Litter samples were air-dried and stored frozen at -15°C .

GM egg masses for these experiments were obtained from USDA-APHIS (Otis Air National Guard Base, Massachusetts). Egg masses were surface sterilized for 5 min using a 1.9% solution of commercial bleach containing Tween 80. Larvae were hatched and reared inside

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