

CHAPTER 2.2

From Genes to Ecosystems: Plant Genetics as a Link between Above- and Belowground Processes

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2.2.1 Introduction

This chapter addresses several key issues regarding the importance of a “genes to ecosystem” approach in considering plant–soil linkages. Firstly, we examine how plant functional traits bridge plant species interactions with soil community dynamics. Secondly, we consider the role of plant genetic variation on soil communities and then examine some of the mechanisms by which plant genetic variation affects ecosystem processes. We subsequently explore how plant–soil feedbacks may be strong evolutionary drivers of change in plant functional traits at local and landscape scales, and conclude by considering some key directions for further research. Taken together, this chapter highlights the genetic linkages between plants and soils (i.e. “the extended phenotype”) that may have important, but hitherto little appreciated, evolutionary implications.

All plant species express phenotypic variation in morphological, physiological, and chemical traits which in turn drive belowground processes. Plant phenotypic variation is driven, in part, by genetic variation, and ecologists are increasingly aware that genetic variation within a species merits much more attention than has historically been accorded (Whitham *et al.* 2006; Johnson & Stinchcombe 2007; Hughes *et al.* 2008; Bailey *et al.* 2009). Intraspecific trait variation in plants influences aboveground processes, including structuring foliar arthropod communities (Wimp *et al.* 2004; Johnson & Agrawal 2005; Crutsinger *et al.* 2006;

Keith *et al.* 2010), providing resistance and resilience to environmental stress and disturbance (Hughes & Stachowicz 2004; Reusch *et al.* 2005; Hughes *et al.* 2009), and promoting resistance to invasion by exotic species (Crutsinger *et al.* 2008c; Velland *et al.* 2010). While the role of genetic variation in primary producers has been shown to impact a variety of aboveground response variables, the relationship between plant genetic variation and belowground processes has been less well explored. Recent work has shown that plant genetic variation is particularly important to consider from a belowground perspective as well, as genetically based plant–soil linkages can have strong ecological and evolutionary consequences (Lankau & Strauss 2007; Lankau *et al.* 2010; Pregitzer *et al.* 2010; Felker-Quinn *et al.* 2011; Madritch & Lindroth 2011). Given the long-term legacy effects of plants on soils, it is essential to understand how plant genetic variation influences belowground processes and the supporting services that ecosystems provide (Daily 1997).

Plants influence soil community composition and ecosystem processes in both agricultural and natural systems (Hobbie 1992; Bever *et al.* 1997; Hooper *et al.* 2000; Diab el Arab *et al.* 2001; Wardle *et al.* 2004; Wardle 2006). Most of this work, until recently, has been focused at the level of plant functional group or species. Variation in the quantity and quality of plant inputs to the soil (both above- and belowground) influences substrate availability

for the soil community, including mutualists, root herbivores, pathogens, and decomposers and their activities, as well as soil food web interactions (Paul & Clark 1996; Wardle *et al.* 2003, 2004; Vandenkoornhuyse *et al.* 2003; De Deyn *et al.* 2004; Kang & Mills 2004; Wardle 2006; Horwath 2007). For example, many studies have documented that soil communities, litter decomposition, and mineralization processes differ in soils beneath dominant tree species (Hobbie 1992; Binkley & Menyailo 2005; Wardle 2006). These differences are often due to species-level variation in traits such as plant growth rate, leaf and root chemistry or production, root exudation or abiotic effects due to variation in canopy or rooting structure (Bever *et al.* 1996; Priha *et al.* 2001; Bartelt-Ryser *et al.* 2005; Grayston & Prescott 2005). An appreciation of the links between variation in plant traits and belowground processes in terrestrial ecosystems (Hobbie 1992; Binkley & Giardina 1998; Hooper *et al.* 2000; Wardle *et al.* 2004) suggests that plant intraspecific genetic diversity could influence the belowground community and associated ecosystem processes based on the same mechanisms that structure plant–soil interactions at the species level (Zinke 1962; Bever *et al.* 1996; Rhoades 1997).

Plant–soil linkages may feedback to influence many aspects of plant communities, including invasibility, plant competitive interactions, and successional dynamics (van der Putten *et al.* 1993, 2001; Casper & Castelli 2003; Reynolds *et al.* 2003; Bonkowski & Roy 2005; Kardol *et al.* 2007; Rout & Callaway 2009; de la Peña *et al.* 2010), and may also have evolutionary implications. For example, the net effects of diverse components of the soil community that either interact with the living plant (including root herbivores, pathogens, mutualists) or plant detritus (heterotrophic decomposers) can result in either positive or negative feedback to plant performance or persistence and feedbacks that can vary through time (Bezemer *et al.* 2006; Kardol *et al.* 2006; Kulmatiski *et al.* 2008; Diez *et al.* 2010). Negative plant–soil feedbacks from accumulation of pathogens or herbivores prevent species from persisting at fixed locations or at high abundances and also promote species co-occurrence (Bever 1994, 2003; Bever *et al.* 1997; Klironomos 2002; Bonanomi *et al.* 2005; Diez *et al.* 2010) while positive plant–soil

feedbacks are mechanisms for persistence or local adaptation (Klironomos 2002; Callaway *et al.* 2004; Johnson *et al.* 2010; Mangan *et al.* 2010). Feedbacks from plants in either direction (negatively or positively) may have important implications for selection and subsequent evolutionary dynamics, which has received little attention in natural systems to date (see van der Putten *et al.* 2001). Moreover, recent advances demonstrate (at both the plant species and clone level) “home-field advantage” for decomposer communities and the processes they mediate and show that plant (species) specificity may exist for processes such as leaf litter decomposition (Ayres *et al.* 2006, 2009; Strickland *et al.* 2009; Madritch & Lindroth 2011; but see St. John *et al.* 2011). Together the plant–soil feedback and “home-field advantage” literature indicate that evolutionary consequences may be predicted based on the linkages between plants and soils.

While still nascent, studies of the relationship between plant genetic variation and soil communities and processes in natural systems often show tight connections. The expectation would be that plant-associated components of the soil community associated with living plant roots would create the tightest linkage (e.g. root pathogens or herbivores, fungal mutualists, as in agricultural systems) to influence soil processes and plant–soil feedbacks. While this indeed may be the case, the studies to date in natural systems have focused on how genetically-based variation in plants affects soil decomposer communities and the processes they mediate (Schweitzer *et al.* 2004, 2008a, 2011a; Madritch & Hunter 2005; Madritch *et al.* 2006, 2009; Madritch & Lindroth 2011). Trait variation at the level of plant phenotype, genotype, genotypic variation, population genetic variation, and genetic divergence (via local adaptation within a species) have all been examined to determine their effects on aspects of the soil decomposer community or on soil processes (see Table 2.2.1 for definitions of genetic terms). These studies have found that intraspecific variation of plant traits can cause decomposer communities to change their composition and/or activity, affect local soil processes, interact with the environment (both abiotic and biotic), and impact plant–soil feedbacks that in turn affect plant performance traits at multiple scales.

Table 2.2.1 Genetic terms used in the genetic-based plant–soil linkage literature**Phenotype**

observed value of a trait for an individual that is a composite of genetic and environment effects

Genotype

genetic individual

Genotypic diversity

number of genotypes within a population; manipulations of clonal genotypes or sib-families in mixture from low to high

Genetic variance (V_g)

the variance in a phenotypic trait among individuals due to genetic differences

Genetic divergence

genetic differentiation between populations within a species due to natural selection or drift; can lead to speciation

(From Lynch & Walsh 1998; Connor & Hartl 2004, Hughes *et al.* 2008.)

2.2.2 The role of plant functional traits in bridging species interactions with soil community dynamics

Functional traits in plants vary both among and within species, and influence associated communities and soil food web dynamics, as well as ecosystem processes that soil communities mediate. Plant traits can directly influence soil processes by altering both biotic (e.g. resource quality and quantity for root-associated organisms) and abiotic conditions (e.g. soil moisture, temperature, and humidity). Moreover, plant traits can have indirect effects on associated communities and their activities by altering conditions that impact the physiology of soil decomposers as well as changing the availability of carbon (C) substrates (and other mineral nutrients). While these direct and indirect links vary in their ability to feedback positively or negatively to affect the fitness of the plant that produced the trait(s) (Binkley & Giardina 1998), the linkage between specific plant traits, soil communities and soil processes indicate that plant soil feedbacks would be predicted to be an important factor affecting genetic variation in plant functional traits (Fig. 2.2.1).

A significant body of work has demonstrated the utility of using plant functional traits in ecology (McGill *et al.* 2006; Westoby & Wright 2006; Corn-

well *et al.* 2008; Hillebrand & Matthiessen 2009; de Bello *et al.* 2010). This may be important for determining aspects of the soil community or ecosystem-level processes (e.g. leaf litter decomposition). Traits are manifested as the phenotype upon which selection acts, and these vary with the individual. Beginning with plant communities (McGill *et al.* 2006), ecologists have come to recognize that plant traits, not necessarily species identity, are the major determinants of community and ecosystem consequences (Wright *et al.* 2004; Cornwell *et al.* 2008). Such trait-based approaches are applicable to any level of biodiversity and often focus on variation at the level of the individual organism to elucidate the effects of biodiversity on communities and ecosystems (Petchey & Gaston 2002, 2006). For instance, several authors include intraspecific variation into their estimates of functional diversity for plant species and its effect on ecosystem processes that when accounted for may change the importance of the species effect (Cianciaruso *et al.* 2009; Fajardo & Piper 2011).

Belowground communities (from herbivores to pathogens to decomposers) are amenable to trait-based approaches, in part, because of their tight associations with plants. The microbial decomposer component of the soil community is difficult to assess in the realm of typical richness indices as microbes often reproduce asexually and swap large functionally important sections of DNA, making “species” an arbitrary definition in the microbial world (Ayala *et al.* 2000). Consequently, microbial ecologists are beginning to focus on the functional traits of belowground communities as their defining characteristic using molecular tools that inform on the functionality of microbial genes (Brussard *et al.* Chapter 1.3; Hackl *et al.* Chapter 2.1, this volume). Green *et al.* (2008) suggest building on the functional trait work developed in plant communities, such as the universal “leaf economics spectrum” described by Wright *et al.* (2004), which uses six traits to explain global patterns of plant nutrient cycling rates, *viz.* leaf mass area, photosynthetic rate, leaf nitrogen (N), leaf phosphorus (P), dark respiration rate, and leaf lifespan. Instead of relying on traditionally-defined functional groups, variation along a continuous spectrum of important traits better defines an organism’s functional role in

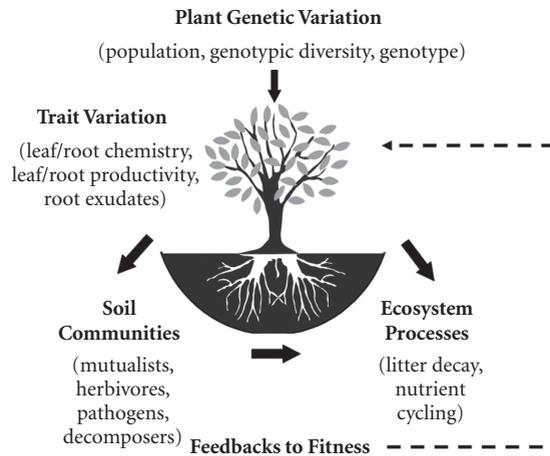


Figure 2.2.1 Schematic illustrating the linkages between plant genetic diversity and soil processes, with evolutionary implications. It demonstrates how plant genetic diversity influences the expression of plant traits that can directly and indirectly influence soil communities and soil processes. Significant variation in soil communities and processes may also feed back to influence the fitness and performance of plant offspring (positively or negatively) to influence population genetic variance. Genetic-based, plant–soil feedback may then be a little-understood mechanism in a larger selective arena that can affect plant population genetics.

an ecosystem. A major challenge in microbial ecology lies in determining which plant functional traits are most important to microbial community dynamics and belowground nutrient cycling phenomena (Green *et al.* 2008; Hackl *et al.* Chapter 2.1, this volume).

The influence of plant functional traits on microbial processes is well-documented, as variation in leaf chemistry partially defines a plant's effect on above- and belowground dynamics. The strong influence of plant structures on belowground processes (Cadisch & Giller 1997) necessitates that the ecology of individual plants has a large influence on the ecology of belowground systems (Bardgett 2002). For instance, the traits that make some plants successful invaders, such as high specific leaf area, rapid growth rate, and elevated nutrient concentrations, often have the effect of increasing decomposition and belowground nutrient cycling rates (Ehrenfeld *et al.* 2001; Allison & Vitousek 2004; Vía *et al.* 2011). Globally, variation in functional traits explains more variation in decomposition rates than do state factors. That is, across global scales, functional trait-driven variation in leaf litter decomposition exceeds climate-driven variation (Cornwell *et al.* 2008). In short, trait-based approaches use direct measurements of expressed phenotypes as a

metric with which to explain community and ecosystem dynamics (Diaz & Cabido 2001; Cornwell & Ackerly 2009). Specific leaf area and leaf N concentration tend to be the two most important leaf-related traits affecting belowground processes (Wright *et al.* 2004; Cornwell *et al.* 2008), especially decomposition and nutrient release. Despite the recent advances linking plant functional traits to belowground decomposition processes, relatively little progress has been made towards identifying the functional traits of belowground organisms that are most important to a diverse array of soil community dynamics (i.e. root herbivores, pathogens, or mutualists) or biogeochemical processes (Green *et al.* 2008). In part, this is due to the inability to identify pathogenic or mutualistic interactions through a functional gene approach (Hackl *et al.* Chapter 2.1, this volume). Nonetheless, advances in trait-based ecology seek to explain belowground communities and processes using fine-scale biotic information.

2.2.3 The role of plant genetic variation on soil communities

The soil community is notoriously difficult to quantify or understand in a holistic manner. Nonetheless, the composition and/or the activity of the soil

community (notably, the heterotrophic decomposer component) have been shown to respond to plant genetic variation. While plant-associated components of the soil community, such as root feeders, symbiotic organisms, and pathogens, may be expected to be the most sensitive to genetic variation in plants, in natural systems the decomposer community has been most examined as it relates to plant trait variation ranging in the scale of variation from phenotype to genotype to genotypic variation to population genetic variance. For example, short-term responses (<3 years) of litter phenotype transplant treatments had little effect on soil bacterial communities (Madritch & Hunter 2005). However, longer-term common garden and field experiments have shown that soil microbial community composition or enzymatic activity can vary based on phenotypic variation in plants. Aspen (*Populus tremuloides*) clones interact with nutrient availability to influence the activity of six extracellular enzymes (including C, protein, and polyphenol aromatic degrading enzymes) as well as rates of soil respiration in litter microcosms (Fig. 2.2.2a, data from the low nutrient treatments only; Madritch *et al.* 2007). Similarly, Schweitzer *et al.* (2008a) found genetic variation in microbial community composition in soils beneath randomized, replicate copies ($n = 3-5$) of five different genotypes of *Populus angustifolia* after 16 years of growth and litter inputs to their associated soils. Each genotype, regardless of position in the common garden, had a similar microbial community in the soils directly beneath each tree, indicating a significant influence of the traits of the tree on soil microorganisms (Fig. 2.2.2b). Similarly, at the population level, forest stands with intermediate gene diversity (i.e. heterozygosity) show a marked shift in soil microbial community composition and extracellular enzyme activity from high or low gene diversity stands, that was correlated with both plant productivity and plant chemistry (Schweitzer *et al.* 2011b). In contrast, the saprophytic fungal community on wood samples (characterized on the basis of fruiting bodies) decomposed in the field for 24 months showed no effects of within-species genetic divergence in *Eucalyptus globulus*, as local properties of wood had a larger effect on fungal composition and richness than did origin of tree provenance (i.e. race) during

the early stages of wood decay (Barbour *et al.* 2009a).

The composition and activity of belowground microbial communities track fine-scale variation in overstory plants. For example, in a 3-year manipulative experiment where aspen litter was reciprocally placed on the forest floor across multiple aspen clones, Madritch and Lindroth (2011) demonstrated that both microbial community composition and extracellular enzyme activity shifted from one resembling the native community to one that was more compositionally similar to the transplanted community. Plots that matched litter genotypes with native soil communities experienced faster litter decay and lost less inorganic soil N than did plots where the litter genotype was foreign to the soil community. These microbial data overall suggest that variation in tree traits, in many cases in terms of plant secondary chemistry, partially determines the community composition or activity of the soil microbial community in both common garden and field studies.

Despite the effects of plant genetic variation or genotype on soil microbial communities, a range of responses to variation in plant traits in other trophic levels within the leaf litter or soil faunal community are apparent. For example, in a leaf-litter amendment study in a common environment Madritch and Hunter (2005) found no effect of nine different oak (*Quercus laevis*) litter phenotypes on the soil micro-arthropod community composition (Acari, Collembola, and other micro-arthropod groups). Similarly, Crutsinger *et al.* (2008b) found that litter-based micro-arthropod communities (Acari, Collembola) extracted from litterbags of *Solidago altissima*, decomposed in a common environment, showed weak effects of plant genotype, and no effects of genotypic diversity, compared to foliar herbivores (and other arthropod guilds) which showed strong responses to both genotype and genotypic diversity (Crutsinger *et al.* 2006). However, the genotypic diversity effects aboveground varied over time and across spatial scales (Crutsinger *et al.* 2008a, 2009). In contrast, leaf litter of two genetically diverged (i.e. locally-adapted) populations of *Eucalyptus globulus* decomposed in a common environment indicated significant differences in richness, abundance, and community

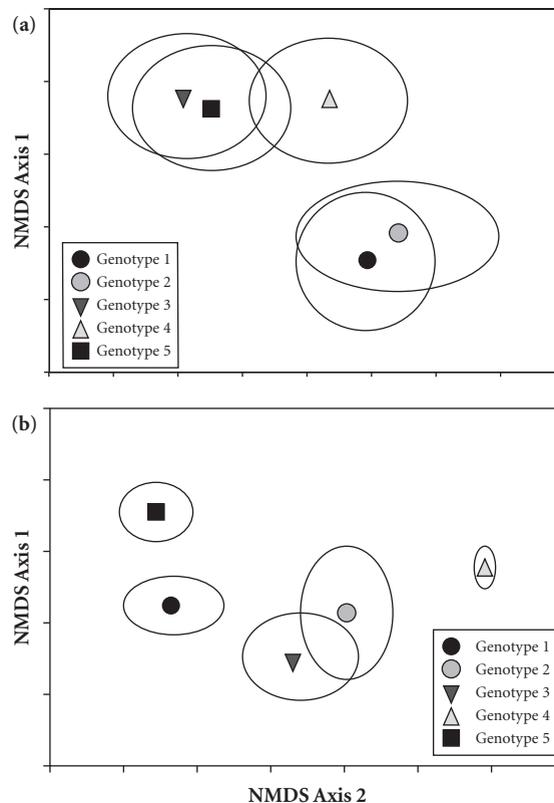


Figure 2.2.2 Experimental results indicate the extracellular enzyme activity or the community composition of soil microbial communities varies beneath trees of different genotypes in common environments. Each symbol (surrounded by ellipses representing $1 \pm$ standard error of the mean) represents the mean activity of six extracellular enzymes in soils associated with *Populus tremuloides* genotypes (a) or the mean microbial community composition in soils associated with *P. angustifolia* (b) genotypes (Bray–Curtis dissimilarity; $n = 3\text{--}5$ replicates/genotype). As this is a distance measure, the non-metric multidimensional scaling (NMDS) axes are unitless. (Data are from Madritch *et al.* 2007 and Schweitzer *et al.* 2008a.)

composition (including Acari, Collembola, and other macro-arthropods) after 4 and 8 months of litter decay (Barbour *et al.* 2009b). These data suggest that the soil micro-arthropod community may respond to plant genetic variation.

2.2.4 The role of plant genetic variation on ecosystem processes

Plants influence soil processes both directly and indirectly through inputs of organic matter that affect local soil communities and the processes they mediate. Within-species variance has been shown to impact soil processes from litter decomposition to total pools and fluxes of soil nutrients, often

reflecting concomitant changes in soil communities. As with soil communities, soil processes related to plant genetic variation interact with environmental variation and show a continuum of plant–soil linkages from weak to strong.

Variation at the level of phenotype or genotype, but not genotypic diversity per se, often results in changes in rates of leaf litter decomposition. Litter phenotype or genotype across multiple plant species affects rates of leaf litter mass loss during early (but not always later) stages of decay when labile constituents of the litter are leached or degraded, as well as affecting nutrient release over time (Madritch & Hunter 2002, 2005; Silfer *et al.* 2007).

For example, genotypes of *Populus angustifolia* × *P. fremontii* tree types differed in decay by 18% as well as demonstrated strong differences in N and P release (Fig. 2.2.3a). The differences in decay were correlated with the concentration of condensed tannin in the foliage (Schweitzer *et al.* 2005). Genotypes of *Solidago altissima* were found to vary in decomposition rate constants by 49%, but this variation was

not as great as that among three species of *Solidago* (Crutsinger *et al.* 2009), indicating that within-species variation in traits may not equal trait variation among species.

While the effects of genotypes in common gardens indicate that genotypic variation can influence rates of litter decay and nutrient release, as would be predicted, genotypic interactions with

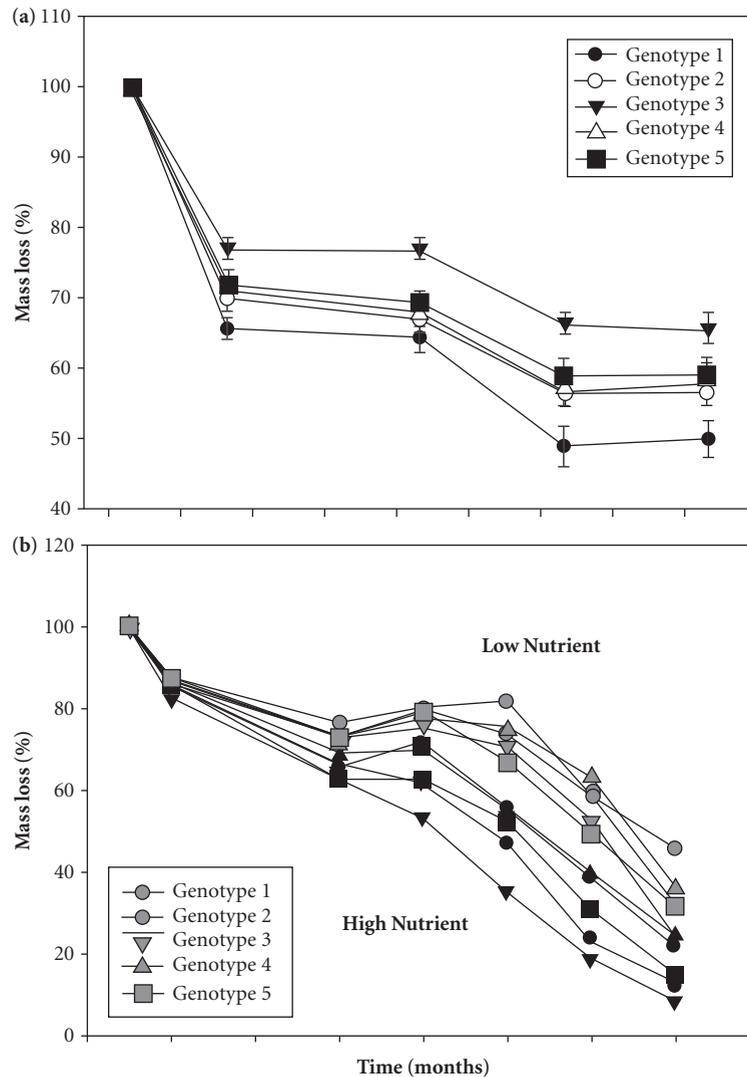


Figure 2.2.3 Experimental results indicate differences in mass loss among genotypes with and without abiotic environmental variation. Genotypes of *Populus angustifolia* decompose at different rates after 24 months in the field (a). Similarly, genotypes of *P. tremuloides* grown under high (black symbols) or low (gray symbols) nutrient treatments decompose at different rates after 13 months in the field (b). (Data are modified from Schweitzer *et al.* 2005 and Madritch *et al.* 2006.)

abiotic and biotic variation also occur. For example, genotypes of aspen grown in high- and low-nutrient environments demonstrate different patterns of foliar chemistry that are influenced by genotype, nutrient treatment, and their interactions over time. This interactive effect of genotype and nutrient treatment on litter chemistry results in genotype \times nutrient treatment interactions in the decay of the same aspen genotypes (Fig. 2.2.3B), as well as the release of N, C, and sulphur (S) from decomposing leaf litter (Madritch *et al.* 2006). When these genotypes were mixed into genotypic diversity treatments to decompose, significant but weak effects of genotypic diversity (three and five genotype mixtures) on decay were found. Fertilization had a much larger relative effect than did genotype for all response variables, indicating that the nutrient availability aspect of the abiotic environment was more important to litter decay than was plant genotype in this study. Therefore, environmental variation interacts with genotype to structure microbially-mediated processes such as litter decomposition, indicating the relative importance of plant genetic variance.

Variation in net rates of N mineralization, net nitrification, or soil nutrient availability can occur in soils associated with plants of varying genetic variation. Individual replicated genotypes from two species of *Populus* (as well as their F_1 hybrids) grown in a common environment indicate that tree genotypes can demonstrate larger variation in annual net rates of N mineralization in their associated soils than the variation between species (Schweitzer *et al.* 2011a), however, as with Crutsinger *et al.* (2009), the range of variance sampled within and across species will determine how general this pattern may be. Moreover, genotype-specific annual rates of N mineralization indicate that processes such as these can have a genetic basis, which indicates that heritable plant traits can repeatedly influence their associated soils. Soil ammonium availability can also vary by litter phenotype treatments (Madritch & Hunter 2002, 2005), although neither soil ammonium nor nitrate change with plant litter treatments of increasing phenotypic diversity (Madritch & Hunter 2005). This then suggests that phenotype composition is more important than phenotypic diversity per se. At the

population level, soil ammonium is correlated with intermediate gene diversity across a gradient of population gene diversity (Schweitzer *et al.* 2011b). While the rates of soil nutrient turnover may vary by plant genetic variation, nutrient uptake also has been shown to vary by plant genotype (Hughes *et al.* 2009) which may also influence overall pools of soil nutrients.

In both common garden and field environments, pools of soil C and N have been shown to vary by plant genotype. Schweitzer *et al.* (2008a) found variation in pools of microbial N and microbial C among 5–8 genotypes each of *P. fremontii*, *P. angustifolia*, and their hybrids in 16-year-old common garden. No differences were found in total soil C or N (Schweitzer *et al.* 2011a). At the level of individual plant clone across a landscape, Madritch *et al.* (2009) found that individual clones of aspen (from 12–40 m²) in the field varied in foliar chemistry that influenced the extracellular enzyme activity of the soil microbial community (relative to adjacent, non-aspen soils). Variation in enzyme activity consequently influenced total pools of soil C and N. These data show linkages from the plant through the microbial community to soil nutrient pools and indicate that plant chemistry, soil microbial communities, and soil processes are all correlated.

2.2.5 The evolutionary implications of plant–soil linkages

While plants can influence many aspects of soils, including soil decomposer communities and the processes they mediate, plant–soil feedbacks in natural systems represent an emerging area of research linking ecology and evolution. Soils and underlying parent material can determine the distribution, population genetic structure and evolution of plant species at large scales (Ellis & Weis 2006; Fierer & Jackson 2006; Alvarez *et al.* 2009). Simultaneously, especially at local scales, plants can influence soil abiotic and biotic properties that feed back to impact plant diversity and succession, persistence of invasive species and overall soil fertility (Ehrenfeld *et al.* 2005; Kardol *et al.* 2006, 2007; Kulmatiski *et al.* 2008; Mangan *et al.* 2010). Whether directly or indirectly, plant functional traits can create conditions that

affect soil communities (i.e. their composition or activity) and decomposition processes that soil communities at least partly regulate (i.e. nutrient depolymerization or mineralization processes). The data to date, described earlier, demonstrate that genetic variation in functional plant traits can influence soil communities and the processes in soil they mediate (i.e. create an “extended phenotype”; Whitham *et al.* 2003). Less is known about how soils may impact the evolutionary dynamics of plant functional traits. For soils to be important factors driving the evolution of functional plant traits, several conditions must be met: there must be genetic variation in the plant population for soils to influence, and plants must respond to such selective forces imposed by soils (Brady *et al.* 2005). Emerging examples linking ecological and evolutionary dynamics provides compelling evidence that an evolutionary response of plants to soils in the form of local adaptation and population-level genetic divergence is possible, and that soil communities may have large impacts on the expression of plant genetic variation.

Recent studies examining “home-field advantage” for a range of community and ecosystem responses in specific “home,” or native conditions, versus “away” conditions are experimental, mechanistic tests that indicate local adaptation. For example, Johnson *et al.* (2010) found that *Andropogon* ecotypes adapt to their local soil via indigenous arbuscular mycorrhizal fungal communities such that mycorrhizal exchange of the most limiting resource is maximized. Because plants have evolved in response to a host of biotic and abiotic soil factors, these results indicate that “soils” act as agents of selection.

In addition to the evolutionary response of plants to arbuscular mycorrhizal fungal communities described in Johnson *et al.* (2010), there are many potential mechanisms by which “soils” may act as agents of selection. It has been proposed that plants are part of a multitrophic selection arena below-ground therefore, as with any evolutionary dynamic, the selective impact and evolutionary response of the interacting species may vary in space, time, and context (*sensu* van der Putten *et al.* 2001; Thompson 2005). Indeed, studies indicating the importance of “home-field advantage” in litter decomposition

(Gholz *et al.* 2000; Ayres *et al.* 2009; Strickland *et al.* 2009; Madritch & Lindroth 2011; St. John *et al.* 2011) show that decomposer communities more efficiently utilize litter nutrients from their “home” than when in “away” conditions. These “home-field advantage” studies provide mechanistic examples of how local litter alters decomposer communities and may act as an important selective force.

When the mechanisms of “home-field” effects are combined with the fitness and performance consequences of feedbacks, the net effect is a plant soil interaction with evolutionary consequences, even if the specific selection gradients are unknown. For example, *Populus* spp. in the western USA vary in plant phytochemical traits that influence rates of leaf litter decay, soil microbial communities, and rates of soil net N mineralization and nutrient availability (Schweitzer *et al.* 2004, 2008b; Rehill *et al.* 2006; Fischer *et al.* 2010). In a greenhouse experiment, Pregitzer *et al.* (2010) planted seedlings from 20 randomly collected *P. angustifolia* genetic families in soils conditioned by various *Populus* species in the field and measured subsequent survival and performance. Even though *P. angustifolia* soils were less fertile overall, *P. angustifolia* seedlings grown in *P. angustifolia*-conditioned soils were twice as likely to survive, grew 24% taller, had 27% more leaves, and 29% greater aboveground biomass than *P. angustifolia* seedlings grown in non-native *P. fremontii* or hybrid soils. Increased survival resulted in higher trait variation among seedlings in native soils compared to seedlings grown in non-native “away” soils. Soil microbial biomass explained more of the variation in seedling performance than soil texture, pH, or nutrient availability, suggesting microbial interactions and feedbacks between plants, soils, and associated microorganisms. Overall, these data suggest that a positive soil feedback helps maintain genetic variance in *P. angustifolia* seedlings, although the specific biotic components of the soil community, and their interactions, that influenced this pattern are unknown.

This framework may be expanded to broad geographic scales, as well as across populations where soils may also act as agents of selection influencing the fitness and performance of plants. Felker-Quinn *et al.* (2011) found that population-level genetic

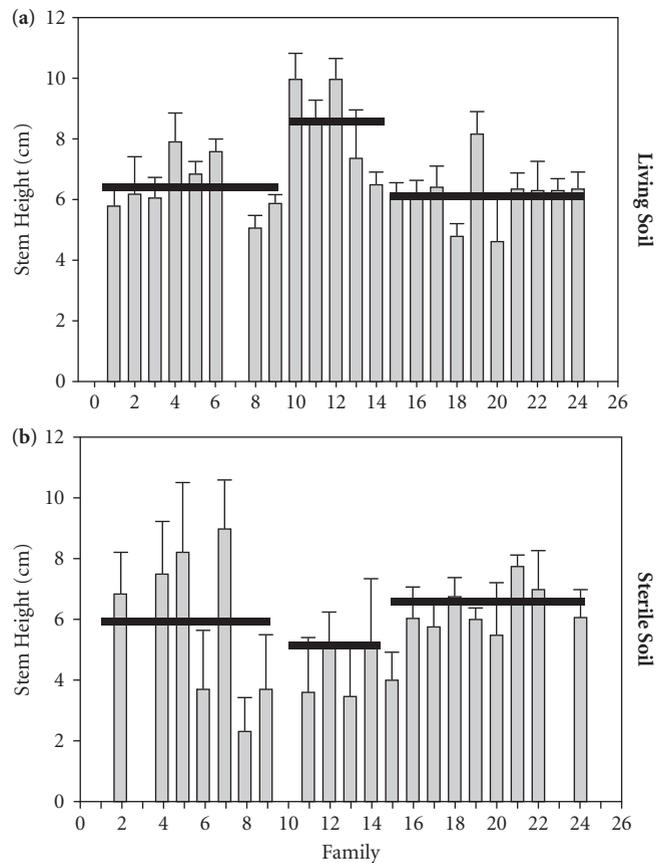


Figure 2.2.4 Experimental results indicate the importance of the soil community in expressing family and population-level variance in tree seedling height. The top panel (a) indicates family and population responses when seedlings were grown in living soil while the bottom panel (b) indicates that the range of genetic variation due to family or population is reduced without the soil community (i.e. in sterile soils). Each bar represents the mean height of an individual family, while the black horizontal bars indicate population level means from each of the three populations of *Ailanthus altissima*. (Data are modified from Felker-Quinn *et al.* 2011.)

variation of three geographically distinct populations of *Ailanthus altissima* resulted in genetic families that vary in growth patterns and phenotypic traits, as determined by growing families of trees from each population in their local and “away” soil. When the seedlings from each family and population were reciprocally grown in soils from each population, with both a live soil and sterile soil treatments, they found that feedbacks from population origin differentially influenced the performance of seedlings. Two populations showed positive feedbacks, whereby seedling performance was enhanced in “home” soils rather than “away” soils, while one population performed better in “away” soils, indicating negative feedback effects. Moreo-

ver, population genetic variance was found when the plants were grown in a live control soil (with an intact soil community), but there was little among-population genetic variance when the seedlings were grown in a sterile control soil for a range of traits (Fig. 2.2.4). These results show that the expression of additive and population level genetic variation depends upon the presence of the soil biotic community and that the interpretation of quantitative evolutionary divergence in plants depends upon the presence of the soil biotic community.

The literature that is based on aboveground systems has commonly found that herbivores and tri-trophic interactions provide important selective gradients for plants (Fritz & Simms 1992; Hunter &

Price 1992; Thompson 2005). However, the soil community is also emerging as an important factor in mediating the evolutionary dynamics of plant functional traits. Both Pregitzer *et al.* (2010) and Felker-Quinn *et al.* (2011) show the importance of within-species genetic variance on plant–soil feedback that is mediated by as yet unknown aspects of the soil community to influence the selection of plant traits in future generations. These data which are some of the first in natural systems to show that genetically-based functional variation in plant traits can influence soil communities and that soil communities affected by functional plant traits can act as agents of selection for aboveground traits through feedbacks. As such, they implicate the soil community as an important regulator of both belowground processes as well as aboveground genetic variation in these systems.

2.2.6 Conclusions and future directions

What do we really know so far? As many of the discussed examples indicate, ecological interactions between plants and soils can result in specific community and ecosystem responses that may feed back to influence trait variation within and among plant populations. Specifically, the studies reviewed here indicate that: 1) plant genetic variance results in shifts in plant phenotypic traits; 2) plant genetic variance impacts decomposer communities and the activity of extracellular enzymes that mediate organic matter dynamics; 3) plant genetic variance impacts aspects of soil C and N cycling; 4) genetic-based “extended phenotype” feedbacks influence plant trait variance (through the soil community), with evolutionary consequences.

Plant traits, at the intraspecific level, may result in predictable impacts on soil communities and aspects of C and N cycling. Plant chemistry, in particular, may constitute potent plant functional traits that influence decomposer soil communities, as indicated by the importance of plant foliar N, lignin, and polyphenol content for many of the earlier examples (*sensu* Grayston *et al.* 1998; Schweitzer *et al.* 2005, 2008b, 2011b; Madritch *et al.* 2006, 2009). Soils change in response to genetic variation in plant traits, directly or indirectly by influencing heterotrophic microbial communities, microbial activities, and soil food web dynamics.

Table 2.2.2 indicates the range of studies and relative strength of responses of genetic-based plant–soil linkages to date. It demonstrates that phenotypic variation occurs across a continuum of genetic variation, from genotype to population-level divergence, which can influence variation in belowground decomposer communities and biogeochemistry, to various degrees. More work is necessary to understand the detailed mechanisms of these linkages including the roles of roots and root-associated communities, root exudates, and genetic-based interactions between C, N, and phosphorus cycles.

While the initial work indicating the importance of genetic-based plant–soil linkages has been done in common environments with limited environmental variation, experiments that incorporate environmental variation (e.g. nutrient addition) in natural systems also indicate that plant genetic factors can drive variation in belowground processes (Madritch *et al.* 2006, 2009; Madritch & Lindroth 2011; Schweitzer *et al.* 2011b). However, it is largely unknown to what extent plant genetic factors interact with large-scale environmental heterogeneity to influence the distribution and activity of soil communities and their resulting nutrient dynamics. Moreover, understanding the importance of plant genetic variance in the context of whole plant community dynamics (i.e. the biotic environment) remains unresolved.

Recent data suggest that genetic-based, plant–soil feedbacks may be an important factor in maintaining plant genetic variation across landscapes. The few studies to date on this topic suggest that positive and negative feedbacks may be an important mechanism for determining population genetic variation. Plant–soil linkage studies may represent a holistic way to assess the evolutionary consequences of multiple interacting feedback loops as plants and soils are players in a multitrophic selection arena (*sensu* van der Putten *et al.* 2001). While the “extended phenotype” of plant genetic variance may feed back to influence subsequent population-level or trait variance (Fig. 2.2.1), other above- and belowground interacting factors, such as herbivory, tritrophic interactions, and plant–plant interactions, are also acting as important selective agents that

Table 2.2.2 Range of studies and the relative responses, to date, examining the effects of plant genetic variation on aspects of soil communities, soil nutrient pools, and fluxes. Empty cells indicate knowledge gaps

	Genotype/individual	Genotypic diversity	Population genetic variance	Genetic divergence (provenance)
Biomass/net primary productivity	Strong	Strong		
Litter decomposition	Moderate	Weak		
Litter nutrient release	Moderate	Weak		
Soil invertebrates	Strong	Weak		Moderate
Microbial community composition	Weak–moderate			None
Extracellular enzyme activity	Strong		Moderate	
Microbial nutrient pools	None–weak		None–weak	
Soil respiration	None–moderate			
Total soil nitrogen/carbon	None	None	None	
Net nitrogen mineralization	Strong			
Nitrogen availability	Strong	Moderate	Moderate	

together will shape the genetic landscape of each interaction. These data along with the strong evidence demonstrating the role of soil communities and plant–soil feedback in mediating plant competitive and successional dynamics (van der Putten *et al.* 1993; Aerts 1999; Bever 2003; Reynolds *et al.* 2003; Bonkowski & Roy 2005; Kardol *et al.* 2006), indicate an important but still little-appreciated role of plant–soil feedback in mediating landscape patterns of ecology and evolution, which may ultimately provide support for the role of adaptive evolution in ecosystem ecology (Matthews *et al.* 2011; Schoener 2011;).

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