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Do high-tannin leaves require more roots?

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Abstract The well-known deceleration of nitrogen (N) cycling in the soil resulting from addition of large amounts of foliar condensed tannins may require increased fine-root growth in order to meet plant demands for N. We examined correlations between fine-root production, plant genetics, and leaf secondary compounds in *Populus angustifolia*, *P. fremontii*, and their hybrids. We measured fine-root (<2mm) production and leaf chemistry along an experimental genetic gradient where leaf litter tannin concentrations are genetically based and exert strong control on net N mineralization in the soil. Fine-root production was highly correlated with leaf tannins and individual tree genetic composition based upon genetic marker estimates, suggesting potential genetic control of compensatory root growth in response to accumulation of foliar secondary compounds in soils. We suggest, based on previous studies in our system and the current study, that genes for tannin production could link foliar chemistry and root growth, which may provide a powerful setting for external feedbacks between above- and belowground processes.

Keywords Feedback · Fine-root growth · Genetics and ecosystems · Minirhizotron · *Populus*

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1 Introduction

Previous work has shown plant–soil feedbacks involving secondary compounds in leaves (Northup et al. 1998; Binkley and Giardina 1998; Kraus et al. 2003). If feedbacks between foliar chemistry and plant growth belowground have adaptive significance then we should find variation in feedbacks at the genetic level. Genetic variation is important because it places plant–soil feedbacks within an evolutionary perspective.

Compounds such as condensed tannins (CTs) may slow down the external process of nutrient cycling (Northup et al. 1998; Kraus et al. 2004; Schweitzer et al. 2004), and may feed back to affect belowground plant carbon (C) allocation strategies (Binkley and Giardina 1998). Plant foliar secondary compounds have previously been tied to decelerated nitrogen (N) cycling (Hättenschwiler and Vitousek 2000; Kraus et al. 2003; Schweitzer et al. 2004). Reductions in soil N availability

may feed back to the plant because N mineralization regulates many plant processes including belowground fine-root dynamics and biomass production (Nadelhoffer et al. 1985; Bloom et al. 1986; Hendricks et al. 2000; Lee and Jose 2003). Resource allocation theory (Bloom et al. 1986) predicts that C allocation will be negatively correlated with N availability, and data from our study taxon (*Populus*; Dickmann et al. 1996; Ibrahim et al. 1998) and broad reviews (Litton et al. 2006) are consistent with this theory. Consequently, plants which produce high amounts of foliar CTs may have an increased need for high fine-root production, C allocation belowground, or N uptake efficiency in order to meet plant nutrient requirements. Without such a compensatory response, lowered litter quality could present a negative feedback to plants through reductions in nutrient availability (see Northup et al. 1998; Binkley and Giardina 1998).

If this feedback loop is genetically based, it could provide a powerful setting for understanding tannins and ecosystem processes within an evolutionary framework. Treseder and Vitousek (2001), Madritch and Hunter (2002), and Schweitzer et al. (2004) have found soil N availability is affected by genetic-based leaf litter chemistry in a diverse array of ecosystems, and much of the variation in leaf chemistry stems from differences in the abundance of compounds such as foliar CTs (see Schweitzer et al. 2004). Genetic-based correlations between foliar tannins and fine root production may provide evidence that in addition to affecting soil N, foliar tannins may also have adaptive significance for belowground C allocation. The intraspecific (defined as an interbreeding complex with significant gene flow; Whitham et al. 2003) scale represents an ideal level for further investigation of feedbacks between foliar CTs and fine-root production because the selection for this belowground subsidy would occur at the genotype level.

Controls over fine-root dynamics also represent a potentially significant pathway through which plant genes can further affect ecosystems. Fine-root dynamics in natural systems affect gene-specific interactions with other belowground organisms (Hirsch et al. 2003; Phillips et al. 2003), represent an important and dynamic component of nutrient and C cycles (Hendrickson and Robinson 1984; Hendricks et al. 1993), and can be under strong genetic control (Pregitzer and Friend 1996).

We measured fine-root production and foliar CT concentration in *Populus* trees growing in a common-garden environment where genetic influences on communities and ecosystems have been experimentally elucidated. For instance, Whitham et al. (2003) and Schweitzer et al. (2004) have shown that CT concentrations are highly responsive to plant genetics. Additionally, Schweitzer et al. (2004) showed that foliar CT in the same trees we measured accounted for up to 65% of the variation in net N mineralization, and that foliar CT:N accounted for ~90% of leaf litter decomposition rate. Our model system represents a unidirectional hybridization gradient between *Populus fremontii* S. Wats. and *P. angustifolia* James. in which F_1 hybrids backcross only with *P. angustifolia*, and genetic distance from *P. fremontii* can be tracked using species-specific restriction fragment length polymorphism (RFLP) markers (see Keim et al. 1989; Martinsen et al. 2001 for details). Because *P. fremontii* is low in CT production while *P. angustifolia* is high and their hybrids are intermediate, within this naturally hybridizing system we can address how aboveground variation in phytochemistry correlates with belowground fine-root production. We hypothesized (1) fine-root production would be positively correlated with aboveground foliar production of CT, and (2) fine-root production would be negatively correlated with proportion *P. fremontii* RLFP markers in our study trees, similar to patterns in CT (see Schweitzer et al. 2004).

2 Materials and methods

Along the Weber River in north-central Utah, USA, higher elevation riparian habitat is dominated by *Populus angustifolia*, the lower elevation riparian habitat is dominated by *P. fremontii*, and in a 13-km zone at their boundaries both parental species and abundant hybrids are found (Keim et al. 1989; Martinsen et al. 2001). The degree of hybridization can be accurately characterized using the fraction of species-specific RFLP markers of *P. fremontii* found in each tree (with 35 species-specific markers; see Keim et al. 1989; Martinsen et al. 2001 for details).

Our work was conducted in experimental common gardens. In 1991, 350 clones, representing 81 naturally occurring genotypes of both parental species, F_1 and backcross hybrids, were randomly planted on 4-m centers in a common garden outside Ogden, Utah, (elev. 1,370 m; 41°11′N, 111°56′W). The RFLP status of each tree was determined in earlier studies (i.e., Keim et al. 1989; Martinsen et al. 2001). The common garden is located at the lower end of the 13-km hybrid zone along the Weber and Ogden Rivers. The soil at the common garden is in the Entisol USDA Soil Taxonomic order. It is composed of ~60% sand, ~30% silt, and ~10% clay (Schweitzer 2002). The site receives approximately 440 mm of precipitation annually. We

were unable to directly measure N availability in this study, but extensive previous work has repeatedly demonstrated that decomposition of leaves from trees in this common garden is strongly controlled by the genetically determined trait of foliar CT concentration, and this in turn reduces N availability (see Driebe and Whitham 2000; Schweitzer et al. 2004; LeRoy et al. 2006). Based on extensive previous work, we have calculated that the N:P ratio of leaves is below 13 (Schweitzer et al. 2005; data not shown), and that more than 50% of N required for aboveground tree growth is returned to the soil through decomposing leaves (based on difference between live and fallen leaves; see Fischer et al. 2004; Schweitzer et al. 2005). Thus, N is likely a limiting nutrient in our system (Sterner and Elser 2002; but note that N:P can be a poor indicator of limitation when nutrients are retained in storage tissues), and is primarily cycled internally.

We measured root production under the canopies of 16 genotypes of varying genetic status: three *P. angustifolia*, four *P. fremontii*, six backcross hybrids, and three F_1 hybrids. The genotypes we measured were randomly interspersed among the 350 clones in the common garden environment so that any potential micro-site effects would be similar among genotypes. Sixteen minirhizotron tubes (one per tree; 6.35 cm inner diameter and 1 m long) were placed under each of the 16 trees of known genotype in the common garden in May 2002. The tubes were placed at –36° to the horizontal to a depth of 55 cm, and positioned so that the deep end of the tube was facing the base of the tree of interest, but at a randomly designated azimuth with respect to each tree. Following tube installation, we trenched trees down to 30 cm, 2 m from the base of the tree, to prevent the influence of genetically different adjacent tree roots. Trenches were double-lined with 0.15-mm-thick polyethylene plastic and back-filled. Such trenches may influence root death and thus could be a source of error in our measurements. However, since all trees were trenched, relative patterns in root production among genotypes should be unaffected by this disturbance. Where minirhizotron tubes emerged from the ground, tubes were painted with a coat of black, then painted with a coat of white, and then covered with a tin can (7.62-cm diameter) to reflect light and reduce heat from solar radiation. Minirhizotron tubes were internally insulated with foam padding between imaging periods.

Minirhizotron images were collected every 2 weeks from 30 June 2002 to 18 November 2002 using a CI-600 (CID, Camas, Wash., USA) high-resolution color scanner head mounted on a rotating motor. The scanner is inserted inside a minirhizotron tube at known depths and orientation, and connected to a laptop computer. At each depth, the scanner head revolves 360° and records the interface between the clear tube and the soil. The result is a 21.6×19.6 cm image. At each tube, three sequential image depths were measured at 0–12, 12–24, and 24–36 cm. Images were analyzed using *RooTracker* imaging software (Duke University, Raleigh, N.C., USA). Observations were dominated by small diameter roots (average 83.1% <1 mm; 95.0% <1.5 mm; 97.9% <2.0 mm). Measurement of minirhizotron tubes in the same year of installation can be problematic due to equilibration of the tube with the surrounding soil (Joslin and Wolfe 1999). However, in highly disturbed riparian soils (Friedman and Lee 2002) roots may recover quickly from disturbance (see Johnson et al. 2001 for studies which have made measurements in the same year as minirhizotron tube installation), and the relative differences in root production among genotypes calculated from these tubes should be unbiased.

Diameters (cm) at 1.4 m height were determined for each tree during fall, 2002, to estimate biomass (g) aboveground. These data were then fitted to a local biomass equation, developed by destructively sampling eight cottonwood trees (six *P. fremontii*, one F_1 hybrid, and one backcross hybrid; diameter range from 7.11 to 37.85 cm) along the nearby Weber River. Each tree was cut and weighed green in the field. Sub-samples of large branches, small branches, and foliage were reweighed before and after being dried at 70°C for 48 h. Least squares regression was then used to develop the allometric equation:

$$\text{Biomass} = -11,330 + 316.43(\text{diameter})^2, \quad (r^2_{\text{adj}} = 0.91,\ P<0.05).$$

We assumed that there were no differences among genotypes in allometry and we feel this assumption is justified because: (1) this equation was similar to another widely used equation developed specifically for *P. balsamifera* ssp. *trichocarpa* in British Columbia (Means et al. 1994); and (2) in earlier studies we have found nearly identical relationships between stem diameter and leaf area for *P. fremontii*, *P. angustifolia*, and hybrid tree types (Fischer et al. 2004; Cox et al. 2005).

Condensed tannin concentrations and foliar N were assayed three times during 2001 (May, July, and August) prior to leaf senescence in order to measure leaves which would affect soil conditions during the growing season of 2002. Averages of these measurements were used for all statistical analyses. Foliar

chemistry was not measured 2002, and this could be a source or error. However, it should also be noted that in exhaustive tests, year-to-year variation in foliar tannin production among genotypes has been found to be minimal (R. Lindroth, unpublished data; Rehill et al. 2005). Briefly, after an exhaustive extraction of leaf tissue in 70% acetone with 1 mM ascorbate at 4°C, CT concentrations were determined with the acid butanol assay using CT prepared from *P. angustifolia* as the standard (see Schweitzer et al. 2004 for further details). Previous work has demonstrated conclusively that use of *P. fremontii* standard produces qualitatively identical results (Lindroth et al., unpublished data). Foliar nitrogen (N) was measured using an elemental analyzer (LECO, St. Joseph, MI, USA), with glycine as a standard.

Statistical analyses were conducted to evaluate three separate objectives: (1) correlation among variables; (2) relative strength of different linear models predicting root growth which included RFLP markers or foliar CT; and (3) plausibility of separate pathways for genetic and CT effects on root growth. For objective one, we used least squares linear regression analyses (SAS JMP version 4.0.4, SAS institute, Cary, N.C., USA). For objective two, we used an information-theoretic approach (Burnham and Anderson 2002) to evaluate controls over fine-root production using five candidate linear models, including an intercept only model. Briefly, the information-theoretic approach uses maximum likelihood theory and the principle of parsimony to assess the strength of evidence for each model in a candidate set of a priori defined models. We used Akaike's Information Criterion, adjusted for small sample size (AICc), an estimate of model likelihood, Akaike weights (w_i), and an ''evidence ratio'' computed from these variables, to simultaneously compare and rank multiple models from a set of a priori candidate models (see Burnham and Anderson 2002). Each measure provides an index of the best model given the data, and the ''evidence ratio'' gives a comparative ''odds'' of the top-ranked model being the best model given the data. Each model incorporated a unique set of independently measured variables hypothesized to be important in the prediction of fine-root production. These variables included proportion *P. fremontii* RFLP markers, foliar CT concentration, and foliar N concentration (Table 1). Models whose ΔAIC (AICc relativized to the lowest value) differed by less than 2.0 were not considered statistically distinguishable, as is common practice (Burnham and Anderson 2002). Finally, for objective three, structural equation modeling (SEM; Pugesek et al. 2003) was used to determine path coefficients (standardized partial correlations) for two effects pathways. The first was a direct pathway between proportion *P. fremontii* RFLP markers and root growth. The second pathway included foliar CT concentration as an intermediate between proportion of *P. fremontii* markers and fine-root growth. Thus, the first pathway estimates correlations between genetics and fine-root growth directly (which may be linked to the effects of genetics on foliar CT concentration), while the second pathway estimates correlations between foliar CT concentration and fine-root growth that are independent of genetic effects on roots. We were unable to include soil N availability in this analysis because it was not measured, therefore any estimates of foliar tannin effects on root growth are likely overestimates (i.e., because there is at least one additional step in the path the correlation is actually more diffuse). The SEM analyses were conducted using AMOS 5.0 (SPSS, Chicago, Ill., USA).

Table 1 Model selection criteria (Burnham and Anderson 2002) for five models predicting fine-root growth

Model	*K*	AIC_c	ΔAIC_c	Likelihood	w_i	Evidence ratio
RFLP markers	3	–41.78	0.00	1.0	0.87	1.00
Combination	5	–37.20	4.58	0.10	0.09	9.88
Foliar CT	3	–35.82	5.97	0.05	0.04	19.74
Intercept	2	–20.20	21.59	2.05E-05	1.78E-05	48,702.64
Foliar N	3	–17.66	24.13	1.24E-05	5.00E-06	173,624.47

The column *K* represents the number of parameters in each model including an intercept and error term. The ''RFLP markers model'' uses only the proportion of RFLP markers as a predictor of fine-root growth. Similarly, the ''Foliar CT'' model used only the foliar concentration of condensed tannins, and the ''Foliar N'' model used only the foliar concentration of N. A ''combination'' model included all three of these factors. An ''Intercept'' only model was also evaluated. Models are ranked from the best (top) to worst (bottom) model based on ΔAICc values [based on Akaike's Information Criterion for small sample size (AICc)] which reflect an index of amount of information lost when approximating truth with the model. The ''RFLP markers'' model is the best model according to all model selection criteria, including: the ΔAICc values (lowest), the likelihood value for the best model (LIKELIHOOD; 1.0), the Akaike weight of evidence (w_i; closest to 1), and the evidence ratio (EVID. RATIO; next best model has a 1:9.88 chance of being better, given the data)

3 Results

We found that the logarithm of fine-root production weighted by tree biomass was negatively correlated with the proportion of *P. fremontii* markers (Fig. 1; r^2=0.77, $P<0.001$) suggesting that fine-root production may be genetically based. The logarithm of the standing length of roots was also negatively related to the proportion of *P. fremontii* markers (r^2=0.78, $P<0.001$).

In agreement with the above findings, we also found a strong relationship between the logarithm of foliar CT concentration and these same RFLP markers (Fig. 2; r^2=0.79, $P<0.001$). This result is consistent with previous studies showing CT concentration in cottonwood leaves is genetically determined (Whitham et al. 2003).

If RFLP markers are correlated with both fine-root production and foliar CT concentration, we should also expect that fine-root production would be correlated with CT concentration. In agreement with this expectation, we found a strong positive correlation between fine-root production and leaf CT concentration (Fig. 3; r^2=0.60, $P<0.001$). Foliar N concentration (a potential indicator of plant nutrient status) showed no significant correlation with RFLP markers (P=0.966), foliar CT (P=0.933), or fine-root production (P=0.961).

Both model selection approaches and SEM suggest some tentative support for a genetic basis to the correlation between fine-root production and foliar CT concentration. Using AICc (a model selection criteria), we determined that the model that included only RFLP markers accounted for 87% of the explanatory weight of the candidate model set predicting fine-root production (Table 1). The best model that contained foliar CT concentration had the odds ~1:10 of being a better model than the best overall model (Table 1; evidence ratio; see Burnham and Anderson 2002). In fact, all models that included foliar CT and N concentrations as factors summarily only account for ~13% of the weights of evidence of models (w_i; Table 1; Burnham and Anderson 2002). Due to the similarities in the ΔAICc values (values within 2.0 of each

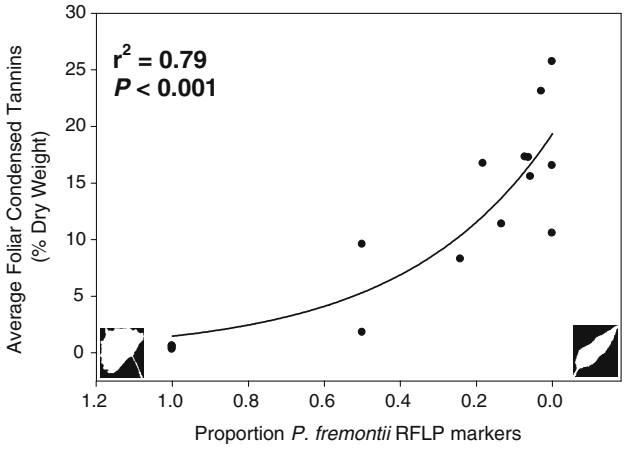

Fig. 2 Average foliar condensed tannin concentration versus proportion *P. fremontii* RFLP markers. Icons represent *P. fremontii* (*broadleaf on left*), and *P. angustifolia* (*narrowleaf on right*). Foliar N was assayed on the same genotypes as minirhizotron measurements in a 12-year-old tree in a common garden environment in northern Utah, USA

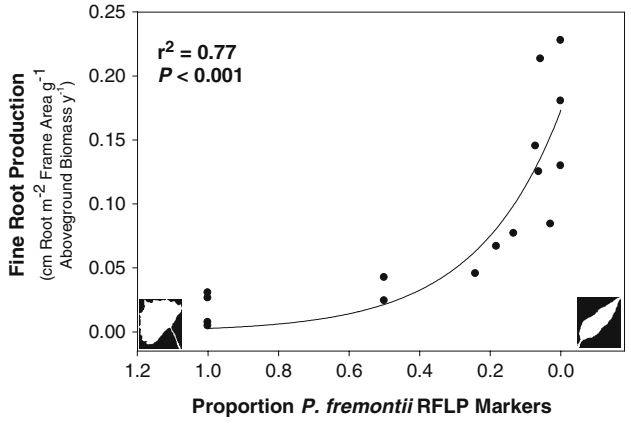

Fig. 1 Relationship between fine-root production weighted by aboveground tree biomass, to proportion of *P. fremontii* restriction fragment length polymorphism (RFLP) markers. Icons represent *P. fremontii* (*broadleaf on left*), and *P. angustifolia* (*narrowleaf on right*). Root production was measured from July 2002 to November 2002 within the upper 36 cm of the soil profile using a minirhizotron approach under 12-year-old trees in a common garden environment in Northern Utah, USA

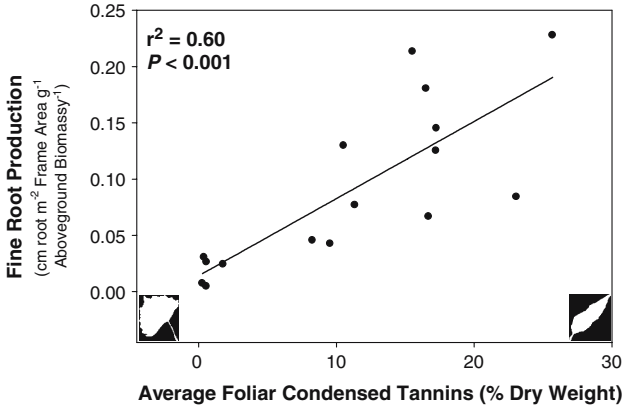

Fig. 3 The relationship between fine-root production and average foliar condensed tannin concentration. Icons represent *P. fremontii* (*broadleaf on left*), and *P. angustifolia* (*narrowleaf on right*). Root production was measured from July 2002 to November 2002 within the upper 36 cm of the soil profile using a minirhizotron approach under 12-year-old trees in a common garden environment in northern Utah, USA. Foliar N was assayed on the same genotypes as minirhizotron measurements

other) among the 2–3 ranked models, these models could not be distinguished in terms of fit (see Burnham and Anderson 2002). Similarly, SEM indicated a correlation coefficient between proportion RFLP markers and fine-root growth of –0.68 (P=0.004), and a correlation coefficient between proportion RFLP markers and foliar CT concentration of –0.87 ($P < 0.001$). In contrast, the partial correlation coefficient (controlling for genetic-based correlations) between foliar CT concentration and root growth was only 0.23 and was not statistically significant (P=0.327), suggesting that a genetic-based correlation effects pathway can account for the relationship between fine-root growth and foliar CT concentrations.

4 Discussion

Investment in foliar compounds known to retard litter decomposition and slow nutrient cycling (e.g., tannins) may result in an increased need for belowground productivity by plants in order to meet plant nutrient requirements. If such a relationship exists, then we might expect to see correlations between fine-root production and foliar CTs as a result of historical selection events or current feedback responses.

While previous studies have shown that high foliar CT concentrations retard net N mineralization in our study system (see Schweitzer et al. 2004), our current study provides evidence for a potential genetic-based feedback response. Our results are not surprising given the effects of reduced N availability increasing fine-root production (Nadelhoffer et al. 1985; Hendricks et al. 2000; Lee and Jose 2003; Bloom et al. 1986) and the widespread effects of tannins on net N mineralization (Kraus et al. 2003). Furthermore, our results demonstrate the covariance of two traits, foliar CT concentration and fine-root production, which would be necessary for genetic-based feedbacks between foliar chemistry and root production to develop. Interestingly, our data on fine-root production do not seem to be a result of simple source–sink responses based on foliar N and carbon availability, but instead better describe a genetic link between traits that could have adaptive significance.

Correlations between fine-root production and CT could have two primary mechanistic explanations that may be difficult to separate: First, litter from an individual tree has strong effects on soil nutrient availability near to that individual and also on root production through changes in soil nutrient status; second, intrinsic, genetically based mechanisms may ensure linkages between higher production of phenolic compounds such as CT and fine-root production. Although the former mechanism may appear unlikely because of the mixing of leaf litter beneath trees within genetically mixed stands, litter inputs beneath an individual tree originating from that genotype may still be great enough and sustained long enough over the life of the tree to produce the response we see in our study trees. The latter explanation may suggest that, evolutionarily, genetic-based litter quality may be coupled to root traits; thus, plants with high CT concentrations in their leaves may allocate more C to roots in order to compensate for the slow nutrient cycling rates associated with the litter and soil organic matter derived from these leaves. These two possible mechanisms are not independent and could both operate together.

Model selection analyses and our SEM approach support the latter genetic-based mechanistic explanation. The model selection results, in particular, imply that the degree of introgression of genes between *P. fremontii* and *P. angustifolia* (Martinsen et al. 2001) most strongly predicts fine-root production in our study trees by a factor of ~10:1 (see Table 1). However, these results are based on analyses of correlations in an experimental environment, and should be tested further through experiments which use artificial litter and tannin additions to test plant and ecosystem responses. For example, selection may have also simultaneously selected for both high tannins and high fine-root growth in *P. angustifolia* independent of interactions between tannins and fine-root growth in ecological space. Additionally, sustained input of foliar tannins to the soil over the lifetime of a tree may better correlate with fine-root production than a single year's foliar tannin concentration. Root-litter tannin inputs could also be important, but we have found no trends in fine-root tannin (varies between 1 and 2%) in previous work (Fischer and Lindroth, unpublished data).

Regardless of the mechanisms discussed above, correlations between leaf secondary compound production and fine-root growth may have important ecosystem and evolutionary implications. First, fine-root production can represent an important component of ecosystem production and nutrient cycles (Hendrickson and Robinson 1984; Hendricks et al. 1993), and influence other belowground organisms (Hirsch et al. 2003; Phillips et al. 2003). Second, integration of a genetic-based foliar chemistry trait that alters nutrient cycling belowground could provide the basis for understanding an important feedback loop that may affect plant fitness. For example, increased root production may come at the expense of reproduction and aboveground growth, and additional costs to the plant

in terms of C allocation. Similarly, manipulation of the soil environment may give plants a competitive advantage (Northup et al. 1998; Binkley and Giardina 1998). Demonstrating such feedbacks at a genetic level is important because they may provide a mechanism for affecting plant evolution and potentially the extended phenotype of individual tree genotypes (Dawkins 1982; Whitham et al. 2003, 2005; Wimp et al. 2005).

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