Soil nitrogen availability varies with plant genetics across diverse river drainages

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Abstract Understanding covariance of plant genetics and soil processes may improve our understanding the role of plant genetics in structuring soils and ecosystem function across landscapes. We measured soil nitrogen (N) and phosphorus (P) availability using ion exchange resin bags within three river drainages across Utah and Arizona, USA. The three drainages spanned more than 1,000 km in distance, 8° of latitude, and varying climatic regimes, but were similarly dominated by stands of *Populus fremontii* (S. Watts), *P. angustifolia* (James), or natural hybrids between the two species. Soil N availability was consistently greater in *P. fremontii* stands compared to *P. angustifolia* stands, and hybrid stands were intermediate. However, we found that the influence of overstory type on soil P availability depended on the river drainage. Our study suggests that, even with a near doubling of mean soil N availability across these drainages, the relative genetic-based effects of the dominant plant on N availability remained consistent. These results expand upon previous work by: 1) providing evidence for linkages between plant genetic factors and ecosystem function across geographic scales; and 2) indicating that plant genetic-based effects on nutrient dynamics in a given ecosystem may differ among nutrients (e.g., N vs. P).

Keywords Ecosystem genetics · Extended phenotype · Genes-to-ecosystems · Ion exchange resin bags · Nitrogen availability · Phosphorus availability · *Populus* · Riparian forests

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Abbreviations

N	Nitrogen
P	Phosphorus
NH_4^+	Ammonium
NO_3^-	Nitrate

Introduction

The introgression of plant genes across hybridizing species may influence ecosystem processes across landscapes (Whitham et al. 2006) and could be an important component in geographic mosaics of genes-to-ecosystems effects (Madritch et al. 2009). Recent studies have demonstrated that plant phenotypic or genotypic variation can be important influences on ecosystem nutrient availability (Treseder and Vitousek 2001; Madritch and Hunter 2002, 2004; Schweitzer et al. 2004; Madritch et al. 2006, 2009), belowground productivity (Fischer et al. 2006, 2007), and plant water-use (Fischer et al. 2004). Many of these studies have focused on the genus *Populus*. Studies that document genetic influences on ecosystem processes are important because they place ecosystem ecology within genetic and evolutionary frameworks. Fine-scale plant genetic covariance with soil processes may suggest that even microevolutionary processes can have major implications for ecosystem function. When species (and their natural hybrids) are dispersed across great geographic distances, genetic variation may also have large, observable effects on landscape-scale processes and patterns (sensu Madritch et al. 2009).

If plant genetic diversity is an important component of ecosystem processes, especially nutrient cycles, we should expect to find broad similarity in the effect of genes and genetic introgression on ecosystems at the landscape scale. Although species effects on soils are ultimately based on the phenotypic differences (e.g., plant traits; Chapin et al. 1997; Scott and Binkley 1997; Binkley and Giardina 1998), effects at finer levels can be addressed by considering the influences of genetic variation within a single species or hybridizing complex. Because species vary genetically across large geographic ranges, understanding consistency in genetic effects enables separation of variation in species effects that may be ascribed to environmental change, but are underlain by genetic influences (Bangert et al. 2006). For example, some genetic hybridization gradients have extremely wide geographic distributions and could have a dominating influence on ecosystem processes over wide geographic extents. High intraspecific variation in plant traits (i.e., phytochemistry) with ecological implications are, in fact, likely to be found in plant hybrid zones because these areas exhibit high genetic diversity associated with the break up of gene

complexes during hybridization (Floate et al. 1993; Rieseberg and Wendel 1993; Rieseberg and Carney 1998; Fritz et al. 2003). Hybrid zones among *Populus* are known to be especially large among forest trees. They can extend greater than 1,000 km (T.G. Whitham - unpublished data), and are common along river drainages stretching from Mexico to Alberta, Canada (Eckenwalder 1984a,b,c).

Previous observational and experimental work along a single river drainage in Utah, USA, demonstrated that soil nitrogen (N) availability was linked with the production of a plant secondary compound (condensed tannin) in *Populus*. Schweitzer et al. (2004, 2008a) have shown that the N cycle may be intricately linked to foliar tannin production through genetic mechanisms. In field, common garden, and laboratory trials, Schweitzer et al. (2004, 2008b) have found plant genetic-based relationships with soil N availability, net N mineralization, and soil microbial communities. In these studies, net N mineralization was highly predictable based on the genetically controlled trait of condensed tannins across a hybridizing complex between two species of *Populus*. Apparently due to foliar condensed tannin inputs to soils, net N mineralization was highest in *Populus fremontii* (S. Watts) forest soils, and lowest in *Populus angustifolia* (James) forest soils (see Bailey et al. 2004; Schweitzer et al. 2004; Rehill et al. 2005). Hybrids between the two species are predictably intermediate in their effect on rates of net N mineralization based on the relative genetic contributions of either parent (a result of both additive and dominant genetic effects—Bangert et al. 2006). Moreover, nutrient dynamics with decomposing litter of all parent species and crosstypes in all zones indicate that nitrogen is most limiting in *P. angutifolia* zones with net immobilization of N for the first year of leaf litter decomposition; in *P. fremontii* zones, N was immobilized only for the first 2 months and then was steadily released over the next 16 months. In contrast, P dynamics in decomposing litter from all types (*P. angustifolia, P. fremontii* and hybrids) demonstrate immobilization of P only during the early stages of decomposition, with P release after 6 months (Schweitzer 2002). All of these patterns correlate with data showing that condensed tannins are lowest in *P. fremontii*, highest in *P. angustifolia* and advanced backcross generations, and intermediate in F_1 hybrids (Schweitzer et al. 2008a). These data

suggest that high molecular weight condensed tannins may result in slowing of leaf decomposition, litter nutrient dynamics and complexation of N in the soil, which has been linked to reduced decomposition and N mineralization in multiple studies (see Kraus et al. 2003, 2004; Schweitzer et al. 2008b). They also show that we might expect minimal effects of plant genetic variation on P dynamics in the same system. Specifically, we might expect geochemical control of P (geologic substrate) rather than biochemical control.

Building upon these previous results, we evaluated the strength of relationships between genetic variation in overstory trees (among two species and their hybrids) and soil nutrient availability in three river drainages across a broad geographic range (a cross-section of the Colorado Plateau in the western USA). We addressed the basic hypothesis that soil nutrient availability varies predictably across genetic hybridization gradients associated with riparian forest trees (*Populus* spp. and hybrids) at the landscape scale. If such genetic effects on ecosystem processes are consistent across landscapes, then this emphasizes the strength of genetic-based, plant-soil linkages in *Populus* hybrid clines in river drainages across the western US. By evaluating patterns in N and P availability, we also addressed the potential complexity associated with genetic-based interactions with fundamentally different element cycles. Specifically, N and P soil availability may not be similarly influenced by variation in genetic-based plant traits since they differ fundamentally in utilization, immobilization, and limitation within the plant and ecosystem (Walker and Syers 1976; McGill and Cole 1981; Schlesinger 1991).

Materials and methods

Across three different river drainages in Utah and Arizona (Fig. 1) that span the length of the Colorado Plateau in the southwestern USA (more than 1,000 km), we identified natural gradients with *Populus* hybrid zones. Each river drainage is dominated by an overstory of *P. fremontii* (Fremont cottonwood), *P. angustifolia* (narrowleaf cottonwood), and the natural hybrids between the two parental species, which range from F_1 hybrids to highly complexed backcross generations (see Eckenwalder 1984a, b, c; Keim et al. 1989; Martinsen et al. 2001 for details) that generally

occur in distinct geographic zones, often delineated by elevation. These systems represent genetic introgression gradients in which *P. fremontii* (a species typically occurring between 1,200 and 1,600 m) contain 35 out of 35 previously identified species-specific *P. fremontii* restriction fragment length polymorphisms (RFLP) markers, F_1 hybrids contain 50% *P. fremontii* markers and backcross hybrid trees contain less than 50% of the markers (see Keim et al. 1989; Martinsen et al. 2001 for details). *Populus angustifolia* (a species typically occurring at >1,600 m) contains 0 of 35 identified markers. The cottonwood overstory for all three river drainages is arranged in distinct geographic zones. Where the ranges of *P. fremontii* and *P. angustifolia* overlap, the forests are dominated by the mixed hybrid swarms in which both parental species and hybrids (both F_1 and backcross generations) co-exist. This pattern of hybridization in a forest tree occurs across most river drainages across the western U.S. dominated by *Populus* spp.(Eckenwalder 1984a, b, c) and allows an examination of the effects of plant genetic factors on communities and ecosystem processes across landscapes (see Whitham et al. 2006; Bangert et al. 2005, 2006, 2008).

Climatic drivers of soil processes (Fig. 1) and soil parent materials differ considerably across the three river drainages. Soil parent material is especially important for P availability, because P may be higher in soils derived with recent igneous origin, and P is generally lower in more weathered, older parent materials (Walker and Syers 1976). The Weber River drainage in northern Utah (41° 11′ N, 111° 56′ W; elevation 1,295–1,646 m) exhibits a typical summer drought pattern with only minor monsoonal precipitation during the summer months, and soil parent materials are largely from sedimentary (Tertiary) and metasedimentary (Precambrian) rocks (Hintze 1974). The Blue River drainage in eastern Arizona (33° 37′ N 109° 06′ W; elevation 1,584–1,951 m) receives most of its precipitation in the summer, with the rest of the precipitation being evenly distributed throughout the year. Soils at Blue River, AZ are influenced by more recently, volcanically derived soil parent materials from the Cenozoic (Reynolds 1988). Indian Creek in southeastern Utah (38° 9′ N 109° 45′ W; elevation 1,646–2,287 m) is considerably drier than the other two sites, but receives both fall-spring and summer precipitation. Soils at the Indian Creek site have a
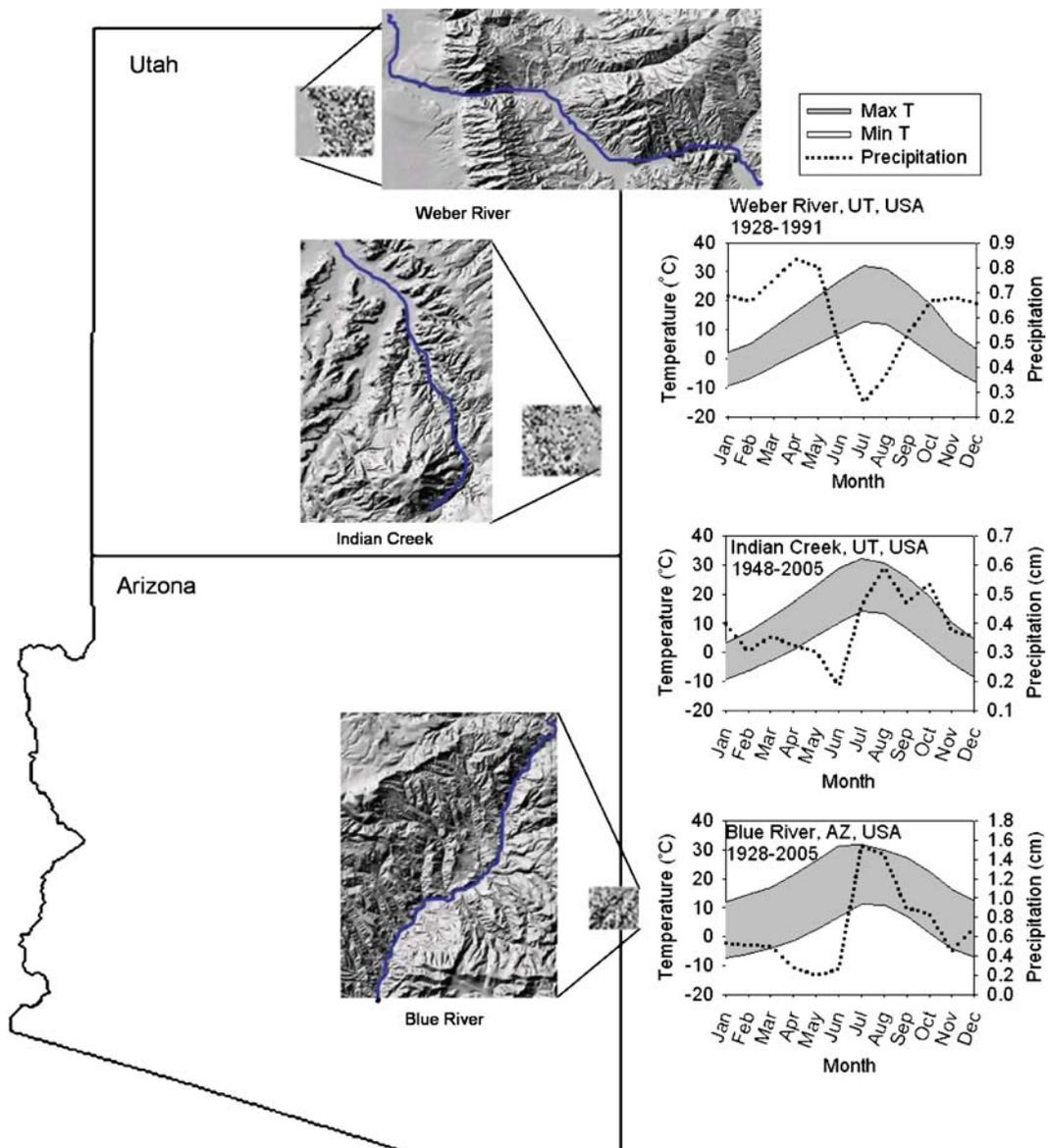
Fig. 1 Cottonwood study sites across the southwestern USA. Study sites transected the Colorado Plateau from the Weber River, UT, to Blue River, AZ. Weather data are from permanent weather stations (http://www.wrcc.dri.edu/ - accessed 11-22-08) proximal to hybrid zones of each river drainage, and represent mean trends over multiple years

mixture of parent materials, including Triassic through Cretaceous sedimentary and Precambrian rocks and Triassic or Tertiary igneous rocks (Hintze 1974). Thus, our sites form a climatic gradient from summer drought (Weber River) to monsoonal precipitation patterns (Blue River), and a geochemical gradient from sedimentary (Weber River) to igneous soil parent materials (Blue River), with the Indian Creek site as the intermediate in both factors. Because each river drainage differs climatically and geochemically, if plant crosstype is unimportant, we would predict differences in nutrient availabilities among drainages irrespective of the dominant plant overstory. In contrast, if plant crosstype strongly shapes the nutrient availability patterns in underlying soils, we would expect consistent rankings of available nutrient pools among overstory plant crosstypes across all drainages.

Nitrogen and phosphorus availability

We used the ion-exchange resin bag technique (Binkley and Matson 1983; Hart and Firestone 1989) to examine soil inorganic N and P availability in forest stands adjacent (1st terrace) to the river channel within each river drainage. At each of the three sites and for two separate incubation periods (summer growing season, June 2002–November 2002 and winter, November 2002–June 2003), we buried 30 mixed-bed, ion exchange resin bags in each "zone" (*P. fremontii*, hybrid, or *P. angustifolia* zones). Resin bags were located randomly within gallery forest stands (within the drip-line) over approximately 6 km per zone in each river drainage, with the resin bags from the winter incubation period placed within 50 cm of the harvested summer resin bags. Large canopy gaps and interspaces were exempted from our sampling. Resin bags consisted of 30 ml (7.8 g oven-dry equivalent) mixed bed ion-exchange resin (Ionac® NM-60 H$^+$/OH$^-$ form type 1 beads; J.T. Baker, Phillipsburg, NJ, USA) in a nylon stocking. The bags were buried at a 10-cm depth in the mineral soil by making a slit in the soil with hand trowel and then carefully inserting the bag into the undisturbed soil profile and tethering the bags to rebar. Bags were incubated for 6 months in situ.

After removal from the field, the resin bags were placed in separate polyethylene bags and kept cool until they were returned to the laboratory (within 7 days). The resin bags were then air dried and the resin beads were removed from their nylon stockings, extracted using 100 ml of 2 M KCl, and filtered. Filter paper was pre-leached with DI and 2 M KCl before filtration. Ammonium (NH$_4^+$), nitrate (NO$_2^-$ + NO$_3^-$), and phosphate (PO$_4^{3-}$) in the KCl extracts were determined on a Lachat Instruments QuickChem 8000 Flow Injection Autoanalyzer (Keeney and Nelson 1982; Lachat Instruments, Inc. 1992, Loveland, CO, USA). Only the summer incubation period extracts were analyzed for PO$_4^{3-}$ because the winter incubation extracts were accidentally destroyed following N analysis. Ammonium was analyzed by an indophenol blue method, and combined NO$_2^-$ + NO$_3^-$ (hereafter refereed to as NO$_3^-$ because of negligible NO$_2^-$ pools) was determined by cadmium reduction followed by diazotizing with sulfanilamide and complexation with N-(1-naphthyl) ethylenediamine dihydrochloride (Keeney and Nelson 1982). Phos-

phate in extracts was determined using a molybdate-ascorbic acid method (QuickChem Method 10-115-01-1-A, Lachat Instruments, Loveland, CO, USA). Annual N availability estimates were produced by summing the inorganic N values over the two consecutive incubation periods. We have no data to suggest significant plant uptake of organic N in our study systems, and this source of N was not included in our analyses.

Statistical analyses

We used a two-factor ANOVA with river drainage and tree overstory type (i.e., pure species or hybrid zone) as fixed effects. All analyses were conducted in JMP 5.1 (JMP DISCOVERY statistical package 5.1, SAS Institute Inc., Cary, NC, USA) using LOG$_{10}$ transformed data to meet normality and homogeneity of variance assumptions. An α of 0.05 was used to denote statistical significance. Post-hoc Tukey's honestly significant difference (HSD) tests were used to separate means for all statistically significant ANOVAs.

Results

Our findings for N availability were consistent with previous work demonstrating tree genetic influences on soil N. A two-factor ANOVA showed that both overstory type (*P. fremontii*, hybrid, or *P. angustifolia*) and river drainage were both significant predictors of soil total inorganic N availability (NH$_4^+$ + NO$_3^-$; Table 1, Fig. 2a, b), and, NH$_4^+$ alone (Table 1; Fig. 2c, d) and there were no significant interaction terms between factors (overstory and river drainage) for either analysis (Table 1). Our model for 12-month NO$_3^-$ availability was not significant at α= 0.05 ($F_{(8, 233)}$=1.91, P=0.06; Fig. 2e–f), however a larger sample size could reveal statistical patterns that we were unable to detect.

Resin inorganic N accumulated over a one year period ranged from 0.102 mg g^{-1} resin in the Blue River, AZ to 0.169 mg g^{-1} resin at Weber River, UT, and ranged from 0.165 mg g^{-1} resin under *P. fremontii* to 0.097 mg g^{-1} resin under *P. angustifolia*. Patterns of inorganic N availability among tree overstory types and across drainages were also strongly driven by summer incubation values (June–November 2002), which were typically three times

Table 1 Two-way analysis of variance output ($F_{(df)}$, P) for analysis of all three river systems and overstory types for both inorganic N and P availability

	Ammonium	Nitrate/Nitrite	Total inorganic nitrogen	Phosphorous
Whole model	$F_{(8, 225)}=3.32$, $P=$**0.001**	$F_{(8, 225)}=1.91$, $P=0.06$	$F_{(8, 225)}=2.25$, $P=$**0.025**	$F_{(8, 224)}=8.09$, $P<$**0.001**
Overstory	$F_{(2, 225)}=4.75$, $P=$**0.001**	NS	$F_{(2, 225)}=3.73$, $P=$**0.025**	$F_{(2, 224)}=1.14$, $P=0.321$
River drainage	$F_{(2, 225)}=6.43$, $P=$**0.002**	NS	$F_{(2, 225)}=4.38$, $P=$**0.014**	$F_{(2, 224)}=19.69$, $P<$**0.001**
Interaction	$F_{(4, 225)}=1.21$, $P=0.305$	NS	$F_{(4, 225)}=0.48$, $P=0.748$	$F_{(4, 224)}=6.46$; $P<$**0.001**

Significant values at $\alpha=0.05$ are in bold

the values for the winter incubation period (November 2002–June 2003; data not shown). Interestingly, NH_4^+ and NO_3^- values were similar for our resin-based N results. More typically, resin-nitrogen values emphasize NO_3^- over NH_4^+ presumably because of the greater mobility of NO_3^- in soil (Binkley and Matson 1983; Hart and Binkley 1985; Hart and Firestone 1989). However, very coarse soils (e.g., riparian soils with coarse fragments and river cobble) may allow greater NH_4^+ movement due to low cation exchange capacity. While relative values of NO_3^- and NH_4^+ are worth noting, our values overall are well within the range of other studies (See Hart and Firestone 1989), and we feel confident that these results may suggest something about mobility of NH_4^+ in coarse, riparian soils.

Fig. 2 Annual estimates of nitrogen (N) availability based on ion exchange resin bags incubated in situ in soils under different overstory trees and in different river drainages. **a**, **c**, and **e**: Mean total inorganic N availability underneath genetically different overstory trees (*P. fremontii*, hybrid, and *P. angustifolia*) across all river drainages for total inorganic N (**a**), ammonium–N (**c**), and nitrate–N (**e**). **b**, **d**, and **f**: Mean inorganic N availability (**b** total inorganic N, **d** ammonium–N, **f** nitrate–N) among rivers transecting the Colorado Plateau from the Blue River, AZ, to Indian Creek, UT, to the Weber River, UT. *Letters* denote significant differences among categories using independent post-hoc Tukey's HSD tests ($P<0.05$). All error bars are one standard error of the mean
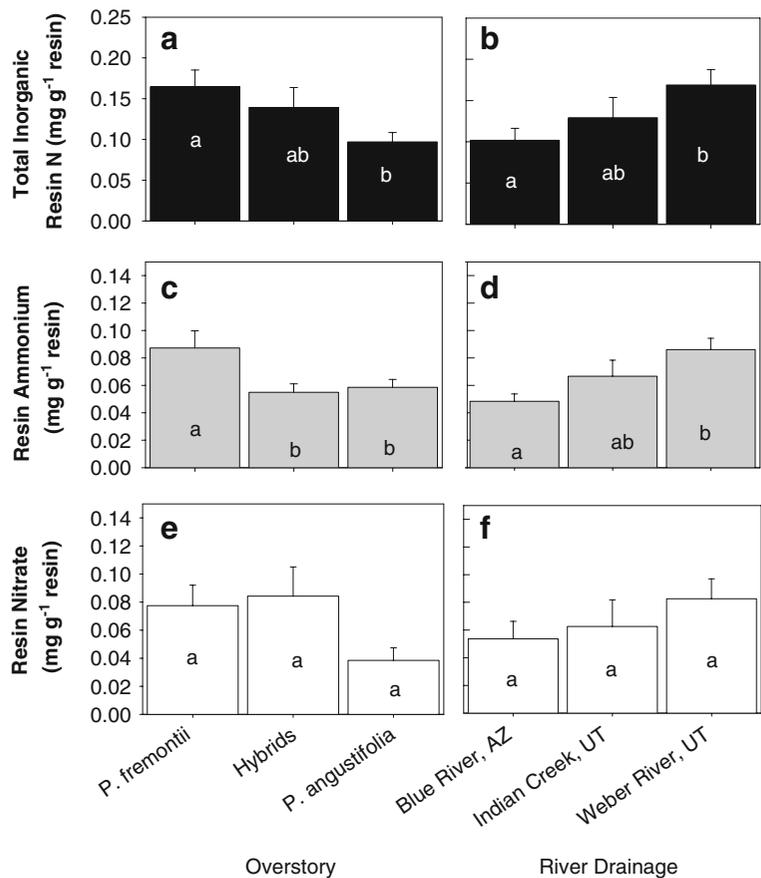
In contrast to soil N availability, the impact of tree overstory type on soil P availability (measured only during the summer growing season) was mediated by river drainage (Table 1; Fig. 3). For example, summer soil P availability was similar across all overstory types in the Blue River and Indian Creek drainages, but higher soil P availability was found under hybrids than the two parental species in the Weber River drainage (Fig. 3). Among river drainages, soil P availability within the Blue River, AZ, was generally higher than in the other river drainages (Tukey's HSD $P<0.05$). Mean resin P values (6-month) across all three overstory types ranged from 0.016 mg P g^{-1} resin within the Indian Creek drainage to 0.039 mg P g^{-1} resin within the Blue River drainage (values comparable with another study using a similar method to simultaneously evaluate N and P availability from resins; Hart and Binkley 1985).

Discussion

Across three river drainages and a range of geologic and climatic variation, we found that soil N availability was consistently higher under canopies of *P. fremontii* compared to under canopies of *P. fremontii x P. angustifolia* hybrids, or *P. angustifolia*. However, we did not find similar consistency with P availability, where overstory type alone was not a significant factor, but interactions between factors and river drainage were significant.

Across all three river drainages, total inorganic N availability decreased ~40% on average from the *P. fremontii* stands to pure *P. angustifolia* overstory (Tukey's HSD $P<0.05$). This is especially striking because soil N availability, as measured by in situ resin bags, nearly doubled across drainages (Tukey's HSD $P<0.05$), yet the pattern among tree overstory types remained the same. In fact, the difference in soil available N between soils with an overstory of *P. fremontii* vs. *P. angustifolia* growing adjacent to one-another were nearly as great as the mean overall differences between river drainages 1,000 km distant (Fig. 2a, b).

Three factors suggest genetic control on the inorganic N availability patterns we observed rather than environmental controls (i.e., temperature and moisture). First, in a previous study, Schweitzer et al. (2004) found identical patterns in net N mineralization in both the field and in laboratory incubations
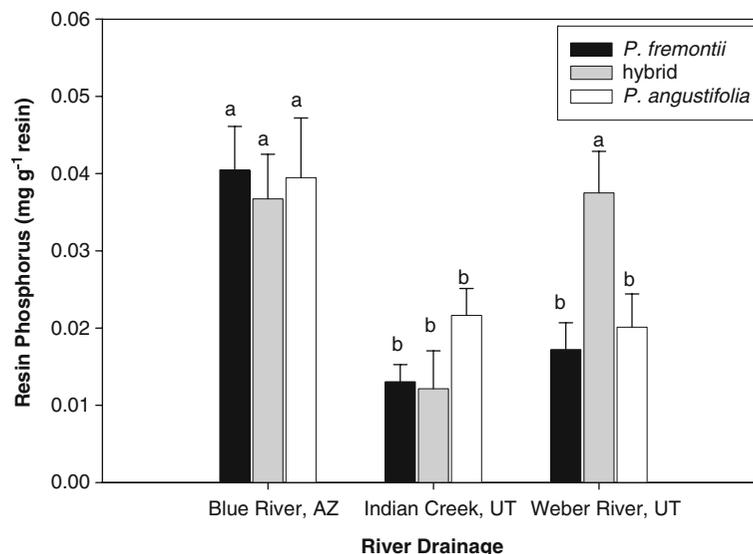

Fig. 3 Soil phosphorus (P) availability during the growing season (June 2002–November 2002) as assessed by in situ ion exchange resin bags under *P. fremontii* (*black bars*), hybrid (*grey bars*), and *P. angustifolia* (*empty bars*) tree overstories in three contrasting river drainages in the Colorado Plateau, USA. Different *letters* denote significant post-hoc Tukey's HSD tests among river drainages within each overstory tree type independently. Blue River, AZ generally had higher soil P availability than Indian Creek, UT or Weber River, UT. However, the hybrid sites at Weber River, UT also showed high P availability, and a significant interaction between overstory type and river drainage occurred ($P=0.029$)

under standard environmental conditions, where net N mineralization was highest in *P. fremontii* stands and lowest in stands dominated by *P. angustifolia*. Schweitzer et al. (2004, 2008b) demonstrated overstory litter quality, decomposition, and plant-mediated soil microbial communities play a larger role in regulating N availability than soil temperature or moisture in these soils. Second, to avoid sampling an environmental gradient that ran parallel to our genetic gradient, we sampled both *P. fremontii* and hybrid trees in the same environment. All *P. fremontii* stands were adjacent to hybrid stands, and in some cases *P. fremontii* stands were actually higher in elevation (max ∼30 m) than our hybrid stands (20 Weber River, UT samples; 15 Blue River, AZ samples). Thus, differences in N availability under *P. fremontii* and hybrid trees (i.e. NH_4^+ availability; Fig. 2c) can likely be attributed to genetic effects between the parent and hybrid tree types, but not differences in elevation (i.e., and corresponding patterns in ambient temperature and moisture with elevation). Third, in two related studies, no significant relationships were found between soil net N mineralization (Schweitzer et al. 2004) or ion exchange resin N availability (Fischer et al. 2007) and soil temperature or gravimetric soil moisture, suggesting N availability patterns are not primarily due to differences in soil temperature or soil moisture under overstory types. These multiple lines of evidence support our hypothesis that overstory tree type within this hybridizing complex largely regulates N availability in their underlying soils rather than abiotic factors.

Soil P availability may be more directly influenced by environment factors because much of the available P pool arises from the weathering of parent material, while the majority of available N results from the microbial mineralization of organic N contained in detritus (Walker and Syers 1976; McGill and Cole 1981; Schlesinger 1991). This paradigm is consistent with our results showing that soil N availability covaried closely with overstory plant type (the dominant source for the plant detrital inputs; Fischer et al. 2007) across all three disparate river drainages, while soil P availability did not. Moreover, previous results from the Weber River suggest that P is not limiting in these soils as P release from decomposition leaf litters across all three zones occurs within months, while N is immobilized for up to 16 months, especially in *P. angustifolia* zones (Schweitzer 2002).

Site factors appeared more closely linked with soil P availability. For instance, P availability was highest in the Blue River drainage whose soils may be influenced by younger, volcanically derived parent materials that are typically high in P (e.g., basalts and andesites; Walker and Syers 1976; Reynolds 1988).

Overall, our data supports the hypothesis that genetic based plant-soil linkages in forests hold across a broad geographic region. Our findings are especially important because hybrid clines in many plant species have large geographic distributions, which may have important and consistent influences on ecosystem processes in riparian areas (e.g., >1,000 km hybrid swarms of *Populus* spp. throughout North America; T.G. Whitham, unpublished data; Eckenwalder 1996). Studies with these and other foundation species and hybridization gradients (e.g., sagebrush and oak species; Wang et al. 1998, 1999; Madritch and Hunter 2002) suggest genetic variation may similarly effect ecosystem function across broad geographical scales through effects on foliar chemistry or other plant traits. However, while some ecosystem processes (e.g., N availability) may be sensitive to genetically based differences in plant traits, some may be less susceptible (e.g., P availability for our study). Overall these data suggest that intra-specific variation at large spatial scales can influence rates of N availability (but not summertime P availability) indicating widespread tight linkages between plants and soils based on heritable plant traits.

References

Bailey JK, Schweitzer JA, Rehill BJ, Lindroth RL, Martinsen GD, Whitham TG (2004) Beavers as molecular geneticists: a genetic basis to the foraging of an ecosystem engineer. Ecology 85:603–608

Bangert RK, Turek RJ, Martinsen GD, Wimp GM, Bailey JK, Whitham TG (2005) Benefits of conservation of plant

genetic diversity to arthropod diversity. Conserv Biol 19:379–390

Bangert RK, Allan GJ, Turek RJ, Wimp GM, Meneses N, Martinsen GD, Keim P, Whitham TG (2006) From genes to geography: a genetic similarity rule for arthropod community structure at multiple geographic scales. Mol Ecol 15:4215–4228

Bangert RK, Lonsdorf EV, Wimp GM, Shuster SM, Fischer DG, Schweitzer JA, Allan GJ, Bailey JK, Whitham TG (2008) Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. Heredity 100:121–131

Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106

Binkley D, Matson P (1983) Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci Soc Am J 47:1050–1052

Chapin FS III, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. Science 277:500–504

Eckenwalder JE (1984a) Natural intersectional hybridization between North American species of Populus (Salicaceae) in sections Aigeiros and Tacamahaca. I. Population studies of P. x parryi. Can J Bot 62:317–324

Eckenwalder JE (1984b) Natural intersectional hybridization between North American species of Populus (Salicaceae) in sections Aigeiros and Tacamahaca. II. Taxonomy. Can J Bot 62:325–335

Eckenwalder JE (1984c) Natural intersectional hybridization between North American species of Populus (Salicaceae) in sections Aigeiros and Tacamahaca. III. Paleobotany and evolution. Can J Bot 62:336–342

Eckenwalder JE (1996) Systematics and evolution of Populus. In: Stettler RF, Bradshaw HD Jr, Heilman PE, Hinckley TM (eds) Biology of Populus and its implications for management and conservation. NRC Research, Ottawa, pp 7–32

Fischer DG, Hart SC, Whitham TG, Martinsen GD, Keim P (2004) Ecosystem implications of genetic variation in water-use of a dominant riparian tree. Oecologia 139:188–197

Fischer DG, Hart SC, Rehill BJ, Lindroth RL, Keim P, Whitham TG (2006) Do high-tannin leaves require more roots? Oecologia 149:668–675

Fischer DG, Hart SC, LeRoy CJ, Whitham TG (2007) Variation in belowground carbon fluxes along a Populus hybridization gradient. New Phytol 176:415–425

Floate KD, Kearsley MJC, Whitham TG (1993) Elevated herbivory in plant hybrid zones: Chrysomela confluens, Populus and phenological sinks. Ecology 74:2056–2065

Fritz RS, Hochwender CG, Brunsfeld SJ, Roche BM (2003) Genetic architecture of susceptibility to herbivores in hybrid willows. J Evol Biol 16:1115–1126

Hart SC, Binkley D (1985) Correlations among indices of forest soil nutrient availability in fertilized and unfertilized loblolly pine plantations. Plant Soil 85:11–21

Hart SC, Firestone MK (1989) Evaluation of three in situ soil nitrogen availability assays. Can J Forest Res 19:185–191

Hintze LF (1974) Geologic map of Utah, Brigham Young University Geology Studies -Special Publication 2. Brigham Young University, Provo. Scale: 1:2500000

Keeney DR, Nelson DW (1982) Nitrogen: inorganic forms. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis, part 2, chemical and microbiological properties, 2nd edn. American Society of Agronomy, Madison, pp 643–698

Keim P, Paige KN, Whitham TG, Lark KG (1989) Genetic analysis of an interspecific hybrid swarm of Populus: occurrence of uni-directional introgression. Genetics 123:557–565

Kraus TEC, Dahlgren RA, Zasoski RJ (2003) Tannins in nutrient dynamics of forest ecosystems: a review. Plant Soil 256:41–66

Kraus TEC, Zasoski RJ, Dahlgren RA, Horwath WR, Preston CM (2004) Carbon and nitrogen dynamics in a forest soil amended with purified tannins from different plant species. Soil Biol Biochem 36:309–321

Madritch MD, Hunter MD (2002) Phenotypic diversity influences ecosystem functioning in an oak sandhills community. Ecology 83:2084–2090

Madritch MD, Hunter MD (2004) Phenotypic diversity and litter chemistry affect nutrient dynamics during litter decomposition in a two species mix. Oikos 105:125–131

Madritch M, Donaldson JR, Lindroth RL (2006) Genetic identity of Populus tremuloides litter influences decomposition and nutrient release in a mixed forest stand. Ecosystems 9:528–537

Madritch MD, Greene SL, Lindroth RL (2009) Genetic mosaics of ecosystem functioning across aspen-dominated landscapes. Oecologia 160:119–127

Martinsen GD, Whitham TG, Turek RJ, Keim P (2001) Hybrid populations selectively filter gene introgression between species. Evolution 55:1325–1335

McGill WB, Cole CV (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26:267–286

Rehill BJ, Clauss A, Wieczorek L, Whitham TG, Lindroth RL (2005) Foliar phenolic glycosides from Populus fremontii, Populus angustifolia, and their hybrids. Biochem Syst Ecol 33:125–131

Reynolds SJ (1988) Geologic Map of Arizona, Arizona Geological Survey Map 26. Arizona Geological Survey, Tucson, scale 1:1,000,000

Rieseberg LH, Carney SE (1998) Plant hybridization. New Phytol 140:599–624

Rieseberg LH, Wendel JF (1993) Introgression and its consequences in plants. In: Harrison RG (ed) Hybrid zones and the evolutionary process. Oxford University Press, New York, pp 70–109

Schlesinger WH (1991) Biogeochemistry: an analysis of global change. Academic, San Diego

Schweitzer JA (2002) Genetic variation associated with natural hybridization in cottonwood affects riparian structure and function. Dissertation, Northern Arizona University

Schweitzer JA, Bailey JK, Rehill BJ, Hart SC, Lindroth RL, Keim P, Whitham TG (2004) Genetically based trait in dominant tree affects ecosystem processes. Ecol Lett 7:127–134

Schweitzer JA, Madritch MD, Bailey JK, LeRoy CJ, Fischer DG, Rehill BJ, Lindroth RL, Hagerman AE, Wooley SC, Hart SC, Whitham TG (2008a) From genes to ecosystems: the genetic basis of condensed tannins and their role in nutrient regulation in a Populus model system. Ecosystems 11:1005–1020

Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Lonsdorf EV, Whitham TG, Hart SC (2008b) Soil microorganism-plant interactions; Heritable relationship between plant genotype and associated microorganisms. Ecology 89:773–781

Scott NA, Binkley D (1997) Foliage litter quality and annual net N mineralization: comparison across North American field sites. Oecologia 111:151–159

Treseder KK, Vitousek PM (2001) Potential ecosystem-level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. Oecologia 126:266–275

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15:1–19

Wang H, Byrd DW, Howard JL, McArthur ED, Graham JH, Freeman DC (1998) Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). V. Soil properties. Int J Plant Sci 159:139–147

Wang H, McArthur ED, Freeman DC (1999) Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IX. Elemental uptake and niche differentiation. Am J Bot 86:1099–1107

Whitham TG, Bailey JK, Schweitzer JA, LeRoy CJ, Fischer DG, Lonsdorf E, Shuster SM, Lindroth RL, Hart SC, Allan GJ, Gehring CA, Keim P, Potts BM, Woolbright S (2006) From genes to ecosystems: how genes structure communities and affect ecosystem processes. Nat Rev Genet 7:510–523