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REGULAR ARTICLE

Soil-mediated local adaptation alters seedling survival and performance

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Abstract
Background and aims Soils can act as agents of natural selection, causing differential fitness among genotypes and/or families of the same plant species, especially when soils have extreme physical or chemical properties. More subtle changes in soils, such as variation in microbial communities, may also act as agents of selection. We hypothesized that variation in soil properties within a single river drainage can be a selective gradient, driving local adaptation in plants.
Methods Using seeds collected from individual genotypes of *Populus angustifolia* James and soils collected from underneath the same trees, we use a reciprocal transplant design to test whether seedlings would be locally adapted to their parental soil type.
Results We found three patterns: 1. Soils from beneath individual genotypes varied in pH, soil texture, nutrient content, microbial biomass and the physiological status of microorganisms. 2. Seedlings grown in local soils experienced 2.5-fold greater survival than seedlings planted in non-local soils. 3. Using a composite of height, number of leaves and leaf area to measure plant growth, seedlings grew ~17.5% larger in their local soil than in non-local soil.
Conclusions These data support the hypothesis that variation in soils across subtle gradients can act as an important selective agent, causing differential fitness and local adaptation in plants.

Keywords Home-field advantage · Local adaptation · Phospholipid fatty acid biomarkers · *Populus* · Soil as selective agent · Plant soil ineractions

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Introduction

Soils are known to act as agents of natural selection, driving genetic structure and specialization within

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plant species. For example, soils that vary in their abiotic and biotic properties can select for certain plant traits, such that plant types perform relatively better in local soil conditions (Waser and Price 1985; Sambatti and Rice 2006; Wright et al. 2006; Pregitzer et al. 2010). Several experiments have demonstrated that plant populations can become locally adapted to extreme soil properties, such as heavy metal and quartz content (Antonovics 2006; Ellis and Weis 2006). Some of the best examples of this are with respect to serpentine soils that are characterized by having lower calcium (Ca) to magnesium (Mg) ratios, as well as lower phosphorus (P) and lower water availability compared to non-serpentine soils, creating gradients in conditions to which plants become adapted (Sambatti and Rice 2006; Wright et al. 2006). Sambatti and Rice (2006) showed that ecotypes of *Helianthus exilis* are locally adapted to serpentine and non-serpentine soils. Seedlings derived from plants growing in serpentine soils had higher survival than seedlings derived from plants growing in non-serpentine habitats when both sets of seedlings were grown in serpentine soils. This differential mortality of the two ecotypes suggests that soils can act as agents of natural selection, causing local adaptation and perhaps speciation in plants. However, extreme soil gradients may not be required for soils to act as strong selective agents on plants.

Relatively subtle differences in soils can also act as agents of natural selection, causing local adaptation in plants (Waser and Price 1985; Schmitt and Gamble 1990; Macel et al. 2007; Johnson et al. 2010; Pregitzer et al. 2010). For example, Waser and Price (1985) showed that *Delphinium nelsonii* became locally adapted over a spatial scale of just 50 m. Examining plants growing in three micro-sites, they performed a reciprocal transplant experiment to show that plants performed best in their home environment. Similarly, Schmitt and Gamble (1990) showed that cleistogamous seedlings of *Impatiens capensis* performed best within 3 m of the parent plant and performance declined at only 12 m from the parent plant, suggesting that plants were adapted to local soil conditions. Similarly, Pregitzer et al. (2010) showed that the narrowleaf cottonwood, *Populus angustifolia,* survives and performs best in local soils within its natural range from within a single river drainage. *P. angustifolia* and the closely related species *P. fremontii* frequently co-occur in Western U.S. mountainous river drainages, with the former growing at high elevations and the latter at low elevations. Further, the two species hybridize and hybrids tend to grow at mid elevations. Using soils collected from high, mid and low elevations (i.e. the ranges of *P. angustifolia*, hybrids and *P. fremontii,* respectively) along the same river drainage, Pregitzer et al. (2010) showed that *P. angustifolia* seedlings, grown in a greenhouse, had higher survival and grew faster in soil from their home (high elevation) range, suggesting that soils were acting as an agent of natural selection, causing *P. angustifolia* to become adapted to local soil conditions.

This study (Pregitzer et al. 2010) demonstrates that micro-site differences in soil may help maintain genetic variation within a site and possibly genetic structure across sites. This process may be particularly important in *Populus* or other clonal species. Both *P. angustifolia* and *P. tremuloides* (quaking aspen) are known to form large clones that can occupy several hectares. Local adaptation to soils may facilitate this type of life history strategy, where several trunks of the same genotype grow in the same area. Plants that are adapted to local soil conditions may have a fitness advantage by cloning and outcompeting invading genotypes. Thus, sites with certain soil characteristics could select for a relatively small subset of genotypes, decreasing genetic diversity at a single site. Conversely, examining a mosaic of soil properties across a larger spatial scale could increase genetic variation among sites.

Here, we examine how soils can be drivers of local adaptation in a riparian forest tree species. While previous research (Pregitzer et al. 2010) examined patterns across soils from two *Populus* species and their hybrids within a single river drainage, we look at soil variation within the range of *P. angustifolia* alone. Using soils collected from beneath five *P. angustifolia* individuals growing in the wild across 65 km, we conducted a reciprocal transplant experiment to test three hypotheses: 1) Soil properties would vary across the five soils, 2) Seedlings grown in local soils would experience greater survival than seedlings planted in foreign soils and 3) Seedlings would grow larger in local soils.

Materials and methods

Seed collection

We collected seed from five, open-pollinated maternal *P. angustifolia* James genotypes growing along the

Weber River, near Ogden Utah, USA. We assumed each tree was a distinct genotype because individual trees were separated by at least 5 km and as much as 20 km. We selected sexually mature trees that did not have a neighboring tree within 15 m to minimize the possible confounding effects of neighboring trees on soil properties. While all trees were sexually mature, tree height ranged from approximately 8 m to 15 m and the distance to the nearest constant water source ranged from 10 m to 250 m. Seeds were collected in July 2006 just before dehiscence. Catkins were collected at multiple locations from the tree canopy, placed in paper bags with a desiccant and stored at 4°C until processed. Seeds were first germinated in plastic Petri dishes on filter paper (Whatman No. 1) and moistened with deionzed water. Dishes were monitored twice a day and watered as necessary. When seedlings were 1 cm in height (~72 h after germination) they were reciprocally transplanted into treatment soils (see methods below) in bookplanters (Tinus Roottrainers, Spencer-Lemaire, Edmonton, Alberta Canada). Ten successfully germinated seedlings (half-sibs) from each maternal genotype were reciprocally placed in each soil type (n=250: 10 half-sib seedlings from five maternal genotypes planted reciprocally into all five soils, Online Resource 1). The bookplanters were placed in a greenhouse, watered weekly and grown at ~22°C and ~15% humidity. We randomly repositioned bookplanters every 2 weeks to minimize micro-site effects.

After 2 weeks of growing in the bookplanters, survival was scored as the number of survivors in each treatment. After an additional 4 weeks (six total weeks) the survivors were scored for seedling height, number of leaves and area of the largest leaf.

Soil collections and analyses

Approximately 40 L of mineral soil was collected from 0–15 cm depth, within 1 m of the trunk, beneath the same trees from which the seeds were collected. Leaf litter, roots and coarse fragments were removed and each soil was thoroughly mixed (Pro-Grow Soil mixer SM10-3, Brookfield, WI USA) to homogenize soil from each genotype. Soils were then placed in bookplanters (each cell measures~4×4×15 cm) with 2 cm of greenhouse potting mix in the bottom of each cell to prevent soil loss.

We assessed various biotic and abiotic parameters of each soil. A sub-sample of each soil was placed on ice, transported to the lab and a portion of it immediately frozen for later analyses; other sub-samples were analyzed within 48 h (see methods below). To determine if soil microorganisms differed by tree genotype, we measured microbial community composition (with neutral- and phospholipids fatty acid analysis [NFLA and PLFA, respectively]), microbial physiological condition (ratio of NFLA to PLFA; Olsson 1999; Bååth and Anderson 2003), microbial biomass (sum of total PLFA), and fungal to bacteria ratios (see Schweitzer et al. 2008 for the complete list of PLFA). A fraction of each soil was immediately frozen and then freeze-dried to evaluate microbial community composition with PLFA and NFLA biomarkers (White and Ringleberg 1998). These soils were extracted with a phosphate-buffered chloroform-methanol solvent (Bligh and Dwyer 1959). Fatty acids were methylated and separated into functional classes of the polar lipids (for PLFA) and the neutral lipids (for NFLA) and analyzed using mass spectrometry gas chromatography (White et al. 1979; Agilent Technologies GC-Mass Spectrometer [6890N GC/ 5973N MSD] Palo Alto, CA, USA). PLFA compounds identified as general bacterial (14:0, i15:0, a15:0, 15:0, i16:0, 10me16, 16:1ω9, 17:0, cy17:0, 18:0) and fungal biomarkers (18:1ω9c, 18:2ω6t, 18:2ω6c) were used to calculate the ratio of bacterial to fungal PLFA concentration in the soils (O'Leary and Wilkinson 1988; Wilkinson 1988; Frostegård and Bååth 1996; Frostegård et al. 1993; Zelles 1999).

The nutrient status of each soil was then evaluated by measuring the total organic carbon (C) and total N content of air-dried soil. The samples were run on a Costech Analytical ECS 4010 elemental analyzer (Costech, Valencia CA, USA) interfaced with a Thermo-Finnigan Delta^{plus} Advantage gas isotope-ratio mass spectrometer (Thermo Fisher Scientific, Inc., Waltham, MA). The pH of each soil was determined in 0.01M $CaCl_2$ solution (Hendershot et al. 1993) using a pH meter (Orion 720A series, Thermo Fisher Scientific, Inc., Waltham, MA USA). Soil texture (percent sand/silt/clay particles) was determined using the hydrometer method (Gee and Bauder 1986).

Statistical analyses

We used two approaches to examine differential survival of seedlings across soil types. We used two approaches because each one provides unique informa-

tion. One analysis tested for a statistically significant difference in survival between soil types, while the other measured the magnitude of differential survival (if any). First, we used an exact test to determine if seedlings survived better in their local soils (Fleiss et al. 2003). For the exact tests, we generated five (one for each tree) 2-by-2 contingency tables for soil type (local and non-local) and survival (live and dead), resulting in a 5×2×2 table. The notation "local" denotes soil from beneath the same maternal genotype while "non-local" denotes soil from beneath the other genotypes (see Online Resource 1 for a graphical depiction of the design matrix and classification of local and non-local soils). Because we compared survival and performance between local and non-local soils, a significant soil effect would provide evidence for local adaptation. We did not test for a significant genotype effect on seedling survival. While it is possible that survival may vary across seedling families, the focus of the paper was on potential influences of the soil. A Breslow-Day-Tarone test was done to test if the effect of the soil varies by tree genotype (i.e. a soil x tree genotype interaction). If the effect of soil on survival varied by tree genotype, it would prevent the estimation of a common odds ratio.

Second, we quantified the magnitude of the effect of soil origin on survivorship by using a Mantel-Haenszel common odds ratio (θ), which measures the relative magnitude of the difference in survival between local and non-local soils (Agresti 2002, 2007). An estimate of θ equal to one suggests that there is no survival difference between local and non-local soils, while estimated θ values greater than one suggest that seedlings were more likely to survive in local soils compared to non-local soils. Further, the difference in θ from one is proportional to the magnitude of the effect of soil on survival.

To test the hypothesis that plants would perform better in their local soils, we first summarized the three response variables (leaf area, seedling height and number of leaves) into a single principal component (PC) score. We analyzed PC1, instead of the individual variables, for two reasons. First, when multiple morphological traits are measured, it is common to use PCA to summarized overall size (Codima and Jolliffe 1996). Second, and perhaps more importantly, summarizing multiple variables into a single PC score controls for the correlation among the original response variables (leaf size, leaf number and plant height). We did not harvest the seedlings to measure total biomass in order to save the plants for a long-term experiment. However, previous work with *Populus* has shown that plant biomass is highly correlated with tree height (r=.87; Felix et al. 2008), leaf area and the number of leaves (r=.95; Isebrands and Nelson 1982). The data were square root transformed when they did not meet normality assumptions. The PC scores were standardized where larger-sized seedlings received larger scores. The first principle component (PC1) explained >68% of the variation in the data and the loadings of all three response variables were greater than 0.80, hence, we used PC1 as the response "seedling size" in the following linear mixed model. We used a linear mixed model for a generalized partially balanced incomplete block design, in which we treated the five trees as random effects and soil as a fixed factor. Our model was: $Y_{ijk}=\mu+\rho_i+\tau_j+\varepsilon_{ijk}$, where Y_{ijk} was the principle component score for each seedling. The symbol μ was the grand mean of principal component scores from all seedlings. The symbols ρ_i and τ_j represented the effects of tree genotype and soil origin, respectively. Finally, the symbol ε_{ijk} represented the error. Using the surviving seedlings from the first project (above), we used the model to test whether or not seedlings grew bigger in local soil compared to non-local soil. For the above analyses, we used SAS Version 9.2 (SAS Institute Inc., Cary NC USA). All assumptions of the linear mixed model were checked using residual diagnostics.

Results

Soils from beneath individual genotypes differed in many physical, chemical and biological properties (Table 1). These results suggest that either the tree genotype influenced the soils in specific ways that could influence the fitness of their offspring or site differences selected for that genotype and its offspring. Soils from beneath each of these trees were sandy-loams (i.e., 54–82% sand). Soil pH ranged between 6.62 and 7.56. Soil organic C concentration, total N concentration, and soil C:N ratios ranged from 3.4–12.5%, 0.22–0.73% and 12.96 to 17.05, respectively. We found nearly a 2-fold difference in microbial biomass (as measured by the total PLFA), a 4-fold difference in the physiological status of the

Table 1 Characteristics of soils collected from beneath each of five individual *Populus angustifolia* genotypes along the Weber River, near Ogden UT. Soil pH, particle size (percentage of sand/silt/clay), total microbial biomass, the ratio of neutral fatty acids (neutral fatty acid lipid analyses; NFLA) and phospholipid fatty acids (PLFA), the ratio of soil fungi to bacteria and soil carbon (C), nitrogen (N) and the ratio of C:N were quantified for each tree

Site	pH	Sand/silt/clay (%)	Microb. Biom.[1]	NFLA/PLFA[2]	Fungal:Bact[3]	Soil C (%)	Soil N (%)	Soil C:N
Xing 4	7.35	62/24/14	37.61	1.07	0.40	4.07	0.22	12.96
SM 1	7.22	61/22/17	67.17	0.364	0.34	4.96	0.37	13.42
PA2	6.62	82/12/5	41.95	1.42	0.40	12.49	0.73	17.05
RPL 9	7.56	74/17/8	38.46	1.33	0.28	3.38	0.25	13.45
RB 17	7.29	54/32/14	37.65	0.80	0.27	4.52	0.27	16.99

[1] Sum of total known bacterial and fungal phospholipid fatty acid (PLFA) biomarkers (nmol/g)

[2] Ratio of sum of neutral lipid fatty acid (NFLA) to PLFA

[3] Ratio of known PLFA fungal biomarkers to known bacterial biomarkers

microorganisms (based on the ratio of NFLA to PLFA) and a nearly 2-fold difference in the ratios of fungi to bacteria among soils taken from beneath individual tree genotypes (Table 1).

Both approaches used to examine survival of seedlings across the soils indicated differential survival between local and non-local soils. The exact test was significant (S=29, p=0.0048), providing evidence that seedlings have higher survivorship in their local soils (Fig. 1a, Online Resource 2). We did not find that the effect of soil on survival varied across tree genotypes (X_4^2=3.0623, P=0.5475, Online Resource 3), suggesting that there was a consistent effect of soil on survival allowing us to estimate the common odds ratio.

The Mantel-Haenszel common odds ratio test, to determine the relative magnitude of the difference in survival between local and non-local soils, indicated that plant survival was approximately 2.5 times greater in local soils. The estimated θ's for the five

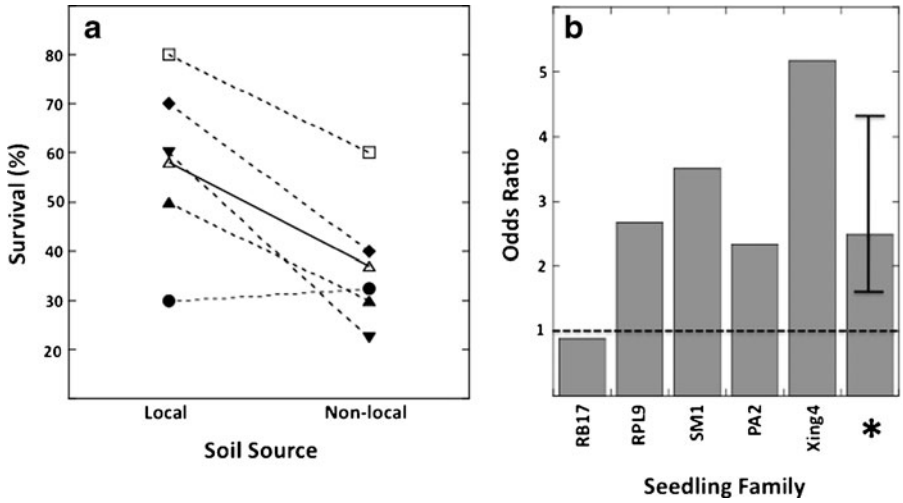

Fig. 1 There were significant differences in seedling survival when half-sibling seed families of *Populus angustifolia* were grown in their local and non-local soils. Panel **a** shows the percent survival of five seedling families when grown in local and non-local soils. The solid line represents the mean survival of all families in local and non-local soils. Panel **b** shows the odds ratios for survival in local and non-local soils for each of the five seed families. In this case, the odds ratio is a ratio of survival in local soils to survival in non-local soils. An odds ratio greater than one suggests seedlings survive better in local soils. The common odds ratio (shown with an *asterisk*), which is the weighted average of the five odds ratios, shows that seedlings are on average 2.5× more likely to survive in local soils compared to non-local soils. The error bar is the asymptotic 95% confidence interval

trees were approximately 0.89, 2.33, 2.67, 3.50, and 5.17. The estimated common odds ratio was 2.48 (the asymptotic 95% confidence interval was 1.29 to 4.77), suggesting that, across all families, seedlings were 2.48 times more likely to survive when grown in their local soil compared to non-local soils (Fig. 1b, Online Resource 3). Because the confidence interval does not contain one, it corroborates the exact test and demonstrates that seedlings have higher survival in their local soils.

Using the first PCA scores in the above linear mixed model (derived from three growth parameters) to compare plant size in local vs non-local soil, we found a trend, suggesting that plants grew larger in their local soil (Fig. 2a; $t_{65.4}=1.98$, $p=0.0517$, Online Resource 3). Even though we did not analyze the individual response variables, each one tended to be greater in local soils (Fig. 2). Measuring the percent increase in the number of leaves, leaf area and plant height, we found that plants growing in local soils were 18%, 20% and 15% larger, respectively, when grown in local soils. Thus, combining survival and performance, our findings suggest that seedlings achieved higher survival and growth when grown in their local soil.

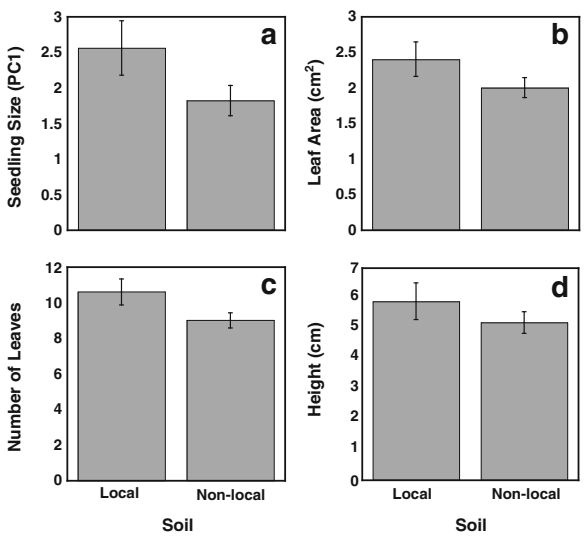

Fig. 2 Different metrics for seedling size in local and non-local soils. Panel **a** shows the scores from the first principal component, which represented "seedling size." It was a composite of plant height, number of leaves and leaf area. Analyzing these principal component scores, we found that seedlings grew larger in local soils. Panels **b**, **c** and **d** show the means of leaf area, number of leaves and seedling height, respectively

Discussion

Our findings show that soils associated with the local genotypes differed in many chemical and biological traits and that seedlings of *P. angustifolia* genotypes achieved 250% higher survivorship and grew ~17.5% larger in their local soils, demonstrating a home-field advantage. While our results of differential performance (Fig. 2) suggested a trend of local adaptation, it is possible that the magnitude of these differences could increase with time. In our measurements of seedling height, we found a difference of approximately 0.7 cm (~15%) after 6 weeks of growing. If the plants had more time to grow this 15% difference could translate into a larger difference in tree size. These results suggest that *P. angustifolia* may become locally adapted to relatively subtle differences in soil properties occurring within the range of the species, within a single river drainage. At this time, it is uncertain whether the differences in survival and performance seen in this study were driven by a combination of chemical properties, biotic properties or both. Data reported here, as well as previous research in this system (Schweitzer et al. 2008), suggests that at least part of the difference is due to biotic components of the soil. Here, the soils collected from underneath the five genotypes differed in their abiotic and biotic properties (Table 1) that might be responsible for differences in survival or performance in their local soils. Microbial biomass, for example, was almost two times higher under tree SM1 compared to the soils from underneath the other trees and fungal biomass differed two fold across the five soils. Further, previous research in this system has shown that individual *P. angustifolia* genotypes are capable of differentially influencing biotic soil properties. In a common garden, that used replicated *P. angustifolia* genotypes, Schweitzer et al. (2008) showed that individual genotypes supported significantly different soil microbial communities. Moreover, this same effect has been recorded for other plant species, indicating that genotypes from within a single species can differentially influence biotic components of the soil (Madritch et al. 2006, 2009; Bezemer et al. 2011). Regardless of the mechanism, local adaptation to soils may affect the genetic structure of *P. angustifolia* and the community and ecosystem properties that the tree influences.

Genetic variation in *P. angustifolia* has shown to be in important driver of variation in community and ecosystem processes (Whitham et al. 2006, 2008). Several studies have shown that individual *P. angustifolia* genotypes support unique ecosystem traits, including soil microbial community composition and ecosystem processes (Schweitzer et al. 2008), community structure and stability of arboreal arthropods (Keith et al. 2010) and trophic interactions (Bailey et al. 2006; Smith et al. 2011). Thus, examining the role of soils in shaping patterns of genetic variation in *P. angustifolia* may give clues into the ultimate causes of these differences in community dynamics and ecosystem processes.

Local adaptation and home-field advantage

Recent studies have demonstrated the importance of "home-field advantage" of locally adapted microbial communities in terms of increasing rates of leaf litter decomposition and nutrient cycles (Ayres et al. 2009; Strickland et al. 2009). For example, soil collected from underneath one plant species was most efficient at decomposing that species' litter and cycling its nutrients (Strickland et al. 2009). Corroborating these findings, Ayres et al. (2009) showed that across 39 plant species, soils tended to decompose "home" litter faster than "foreign" litter. These studies suggest that microbial communities may be selected for and display some adaptation to their local environment. Together, these studies demonstrate the specificity of locally adapted microbial communities to ecosystem processes associated with interspecific plant variation; recent evidence is also showing that this occurs with intraspecific plant variation.

Populations and seedling families from within a single plant species also demonstrate the importance of locally adapted microbial communities to positively impact soil processes and plant performance. For example, Johnson et al. (2010) examined the grass *Andropogon gerardii* from three different field sites and found that plant fitness was consistently highest in home soil with co-adapted arbuscular mycorrhizal fungal communities. This demonstrates that plant populations planted in their native soils have a "home-field advantage," that seems to be driven by a biotic component of the soil. Similarly, the data reported here demonstrates that *P. angustifolia* seedlings have higher survival and growth in their local soil. Together, these studies demonstrate that there is sufficient variation in the soils from beneath a single plant species to promote differential plant fitness (irrespective of what influenced the soils, the genotype or site differences). While these studies have shown a home-field advantage of plants living in local soils, other studies have shown a home-field disadvantage. Seedlings of *Prunus serotina* have been shown to have lower survival and performance when growing relatively near an adult conspecific (Packer and Clay 2000, 2003). Some studies have suggested that asexually reproducing plants (Ronsheim 1996; Bever et al. 1997) and plants at high elevations (Reynolds et al. 2003) will tend to become adapted to local soils, while plants that primarily reproduce sexually from lower elevations will be maladapted to local soils (Ronsheim 1996; Bever et al. 1997; Reynolds et al. 2003). Because this study was conducted with *P. angustifolia*, which primarily reproduces asexually, at elevations between 1,500 m and 2,200 m, we expected and saw adaptation to local soil conditions. While these patterns seem consistent with previous research, it is important to note that a lot of work on local adaptation to soils and plant-soil feedbacks has focused on interspecific variation. Previous studies have compared plant survival and/or performance to other plant species growing in the same soil. This study, by contrast, examined patterns of survival and performance relative to other individuals of the same species.

Intraspecific plant-soil feedbacks

Our results demonstrate that *P. angustifolia* is locally adapted to its local soil. Two, non-mutually exclusive phenomena may be driving this pattern. First, maternal trees may have been pre-adapted to local soil conditions. In other words, of the multiple trees that may have had an opportunity to colonize a particular location, the maternal tree may have survived and grown to maturity because it was able to succeed in the local soil conditions. Because of the relatedness among parents and offspring, it makes sense that seedlings would survive and perform well in soils near the parent tree. A second possibility is that the maternal trees mediated the soil properties that fostered higher survival and growth in their offspring. Previous work in this system (Schweitzer et al. 2008, 2011) and other systems (Madritch et al. 2006; Bezemer et al. 2011) has shown that genotypes are

able to differentially mediate soil properties, including biotic communities, thus the differences in soil properties as seen in this study may be at least partially driven by plant genotype. If individuals, from within a single species, are able to differentially shape soil characteristics which then have fitness affects for the individual and/or its offspring, it would be the first study to our knowledge to demonstrate plant-soil feedbacks at the level of intraspecific variation in trees. Further experimentation is required to differentiate between these two hypotheses. However, these data demonstrate important steps to understanding the role of biotic and abiotic soil properties in shaping patterns of local adaptation.

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