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Genetic variation in tree leaf chemistry predicts the abundance and activity of autotrophic soil microorganisms

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Abstract. Genetic variation in the chemistry of plant leaves can have ecosystem-level consequences. Here, we address the hypothesis that genetic variation in foliar condensed tannins along a *Populus* hybridization gradient influences soil ammonia oxidizers, a group of autotrophic microorganisms that perform the first step of nitrification and are not dependent on carbon derived from plant photosynthesis. Evidence that genetically based plant traits influence the abundance and activity of autotrophic soil microbes would greatly expand the concept of extended plant phenotypes. We found that increasing foliar condensed tannin concentration reduced rates of soil nitrification potential by ~75%, reduced the abundance of ammonia-oxidizing archaea by ~66%, but had no effect on ammonia-oxidizing bacteria. Other indices that often drive nitrification rates, including soil total nitrogen, foliar nitrogen, and soil pH, were not significant predictors of either the activity or the abundance of ammonia oxidizers, suggesting genetic variation in foliar condensed tannins may be the dominant regulating factor. These results demonstrate the condensed tannin phenotypes of two different tree species and their naturally occurring hybrids have extended effects on a key ecosystem process and provide evidence for indirect genetic linkages among autotrophs across at least two domains of life.

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INTRODUCTION

There is growing evidence that intra- and inter-specific genetic differences in plant chemistry can affect the structure and function of above- and belowground microbial communities (Silfver et al. 2007, Bailey et al. 2009, Madritch and Lindroth 2011, Lamit et al. 2015). For example, genotypic differences in foliar condensed tannins (CTs) exert a strong influence on both the composition of microbial communities (Schweitzer et al. 2008*a*, 2011) and the key ecosystem processes they perform, including rates of leaf litter decomposition and nitrogen (N) mineralization in terrestrial (Schweitzer et al. 2004, Madritch et al. 2006) and aquatic ecosystems (Compson et al. 2018). This evidence supports the idea that genetic variation in plants can have

far-reaching consequences on diverse biological communities (Whitham et al. 2012, Crutsinger 2016, Des Roches et al. 2018), yet the effects have thus far been restricted to heterotrophic organisms such as herbivores and decomposers that are directly dependent on carbon fixed by plants through photosynthesis.

Soil ammonia oxidizers are autotrophic microorganisms that perform the first and rate-limiting step in nitrification, the conversion of ammonia (NH_3) to nitrate (NO_3^-), a process that regulates the retention of N in terrestrial ecosystems. At first glance, soil ammonia oxidizers should be insensitive to genetic variation in tree leaf chemistry because they are chemoautotrophs that fix carbon directly from CO_2, and thus are not dependent on carbon derived from plant photosynthesis. However, plant chemistry may have an indirect effect on soil ammonia oxidizers. High concentrations of CTs in leaf litterfall reduce rates of soil N mineralization (Schweitzer et al. 2004), the conversion of organically bound N to inorganic NH_3, which reduces substrate supply to soil ammonia oxidizers and could affect both their activity and abundance.

Several lines of evidence indicate that inputs of leaf litter with high concentrations of CTs can reduce soil nitrification rates (Hattenschwiler and Vitousek 2000, Kraus et al. 2003, Schweitzer et al. 2008b), yet the influence of foliar condensed tannins on the abundance of soil ammonia oxidizers remains unclear. This knowledge gap exists in part because, within the last decade, evidence has accumulated for a previously unknown, large, and nearly ubiquitous group of soil ammonia oxidizers in the domain Archaea (Francis et al. 2005, Nicol and Schleper 2006). Scientific consensus from the late 19th to the early 21st centuries held that a small group of bacteria within the phylum Proteobacteria were solely responsible for oxidizing NH_3 to nitrite, the first step in nitrification (Nicol and Schleper 2006). More recent studies indicate that ammonia-oxidizing archaea (AOA) in the Thaumarchaeota outnumber ammonia-oxidizing bacteria (AOB) in most soils (Leininger et al. 2006, Adair and Schwartz 2008), and that AOA may dominate over AOB in controlling nitrification rates in terrestrial ecosystems with low-to-moderate N availability (Carey et al. 2016, Hink et al. 2018). However, the environmental factors controlling the relative abundance of AOA and AOB are only beginning to be understood, as are their relative contributions to rates of soil nitrification (Taylor et al. 2012, Lu et al. 2015, Hink et al. 2018).

Linkages between genetic variation in plants and the abundance and activity of autotrophic soil microorganisms remain largely unstudied and, if demonstrated, would extend the importance of plant gene expression as an organizing and predictive force governing the structure and function of terrestrial ecosystems. Here, we examine the influence of genetic variation in tree foliar chemistry on the activity and abundance of ammonia oxidizers, a key functional group of soil autotrophic microorganisms, along a naturally occurring *Populus* hybridization gradient in northern Utah, USA. Previous work along this hybridization gradient and in nearby common gardens has demonstrated that foliar CT concentrations vary predictably with plant genotype and hybrid status, that foliar CTs reduce rates of leaf litter decomposition and soil net N mineralization, and that foliar CTs exert a strong control over the composition of heterotrophic soil microbial communities (Schweitzer et al. 2004, 2008a, 2011). Based upon this prior research, we hypothesized the abundance and activity of soil AOA and AOB would be lower in forest stands composed of *Populus* genotypes with high foliar CT concentrations. Support for this hypothesis would further extend the influence of plant genetics on ecosystem functioning and demonstrate for the first time that genetic variation in a foundation tree species can influence the structure and function of soil autotrophic microorganisms with no dependence on plant carbon inputs to soil.

METHODS

Hybridization gradients between *Populus fremontii* and *P. angustifolia* are common along rivers throughout the western United States, where stands at lower elevations are composed entirely of *P. fremontii* with foliar CT concentrations generally <1%, and higher elevation stands are dominated by *P. angustifolia* with up to ten times higher concentrations of foliar CT (Rehill et al. 2006). These two species hybridize freely where their distributions overlap such that

stands at middle elevations are composed of *P. fremontii*, *P. angustifolia*, their F_1 hybrids, and complex, unidirectional backcrosses between F_1 hybrids and *P. angustifolia*. Stands of trees within this hybrid zone have high genetic diversity (Whitham et al. 1999, Schweitzer et al. 2008b, 2011) and a wide range of foliar CT concentrations (Schweitzer et al. 2004, Rehill et al. 2006).

We collected foliage and soil samples from nine gallery forest stands along a naturally occurring *Populus* hybridization gradient within the Weber River drainage of northern Utah, USA (41.2°N, 112°W). The nine stands were spread across three zones (Fremont, hybrid, and narrowleaf) with three stands in each zone. The Fremont zone along the lower reach of the Weber River consisted of gallery forest stands composed entirely of *P. fremontii*, and the narrowleaf zone along the upper reach consisted of stands dominated by *P. angustifolia*. The hybrid zone was in between, with stands containing primarily F_1 hybrids of *P. fremontii* and *P. angustifolia* and complex backcross hybrids between F_1 hybrids and *P. angustifolia*. Each of the nine stands was dominated by cottonwood trees of similar size (20–30 m tall) and density (~650 stems/ha; Fischer et al. 2007) and was separated from each other by at least one km, spanning a linear distance of ~100 km, and an elevation gain of ~500 m (Schweitzer et al. 2004). We selected a central point in each stand and collected live foliage samples from the six nearest mature canopy trees to that point. Six 0–10 cm mineral soil samples were also collected from each stand within the area between the central point and the six sampled trees.

Foliar condensed tannin and nitrogen concentrations

Within each stand, fully expanded sun-lit leaves were collected mid-growing season from four cardinal directions on each of six trees with a pole pruner, placed on dry ice, lyophilized, finely ground, and stored at −20°C until chemical analysis. Foliar CT concentrations were determined by sequentially extracting finely ground leaf samples with 70% acetone +10 mM ascorbic acid and then assaying the extracts with the butanol-HCl method (Porter et al. 1986) using purified CT standards from *P. angustifolia*. Foliar N concentrations were determined on subsamples of the same finely ground leaf samples by combustion with an elemental analyzer (Thermo Finnigan, San Jose, California, USA). We used CT concentrations from live leaves as a proxy for inputs of CT from leaf litterfall. Previous work along this hybridization gradient demonstrated that CT concentrations in green leaves explain nearly 90% of the variation in annual litterfall CT input to soil (Schweitzer et al. 2004).

Potential nitrification rates and soil chemistry

Mineral soil samples ($n = 6$ per stand) were subdivided upon collection with a portion of each sample placed on dry ice in the field and stored at −80°C until DNA extraction and analysis. The remaining portion of each soil sample was sieved to <2 mm and stored at 4°C until analyzed for gravimetric water content, nitrification potentials, pH, total organic carbon, and total N concentrations.

We conducted nitrification potentials (Hart et al. 1994) on subsets of the six mineral soil samples collected from each of the nine forest stands. We estimated maximum nitrification rates (V_{max}) by aerobically incubating soil samples in 250-mL Erlenmeyer flasks on an orbital shaker at 180 rpm for 24 h at 23°C with optimum water, NH_4^+–N, and PO_4^{3-}–P availability, removing 10 mL samples from each flask at 2, 4, 22, and 24 h (Hart et al. 1994). Solutions were analyzed for NO_3^-–N with a Lachat Instruments flow-injection autoanalyzer (Loveland, Colorado, USA).

Soil pH was determined in 1:2 (weight to volume) suspensions of air-dry soil to 0.01 M $CaCl_2$ solution (Hendershot et al. 2007) using an Orion 720A pH meter (Allometrics, Baton Rouge, Louisiana, USA). Soil organic C and soil total N concentrations of finely ground, oven-dried soil samples were determined by combustion at the Colorado Plateau Stable Isotope Facility (Northern Arizona University, Flagstaff, Arizona, USA).

Archaeal and bacterial amoA gene abundance

We estimated the abundance of AOA and AOB across the *Populus* hybridization gradient by quantifying the abundance of archaeal and bacterial versions of the *amoA* gene in soil samples collected from each of the nine stands. The *amoA* gene encodes the subunit containing the

active site of ammonia monooxygenase, an enzyme essential for autotrophic ammonia oxidation. We isolated DNA from 0.5 g of frozen mineral soil using the PowerSoil DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, California, USA) with an additional purification step via ethanol precipitation. All extractions were standardized to 5 ng DNA/μL by dilution in Tris-EDTA buffer. Gene copy number of archaeal and bacterial *amoA* per sample was determined with a DNA Engine Opticon Real-Time PCR system (Bio-Rad, Hercules, California, USA) by amplifying archaeal *amoA* with Arch-amoAF and Arch-amoAR primers (Francis et al. 2005) and bacterial *amoA* with amoA1F and amoA2R primers (Rotthauwe et al. 1997). Samples were run in duplicate, with duplicate runs per sample averaged to yield final gene copy numbers. Standard curves of known archaeal or bacterial *amoA* concentrations (Adair and Schwartz 2008) were included in each qPCR run, and purity of PCR product was verified with melting curves. Amplification efficiency for both archaeal and bacterial *amoA* primer sets was ~85%. Although less than ideal, this should not affect our conclusions because the efficiencies were similar for AOA and AOB, and we were most interested in comparing the relative responses of these two groups of microorganisms.

Data analysis

We used ordinary least-squares regression to determine whether stand-level nitrification potential, archaeal *amoA*, or bacterial *amoA* varied significantly as function of stand-level estimates of foliar CT concentrations. We also used ordinary least-squares regression to examine whether other soil and foliar characteristics were significant predictors of variation in nitrification potential, archaeal *amoA*, or bacterial *amoA*. Our experimental unit for these analyses was the forest stand because tying the influence of a particular tree to an individual soil sample was not feasible, especially in hybrid zone stands. Prior to performing statistical tests, we selected a significance level (α) of 0.10 due to small sample sizes (*n* = 9 forest stands) for all regression analyses.

We used one-way analysis of variance (ANOVA) to examine how soil samples from Fremont, hybrid, and narrowleaf zones differed in the ratio of archaeal to bacterial *amoA* gene abundance. Our experimental unit for this analysis was the individual soil sample, with zone (i.e., pure Fremont, hybrid, and pure narrowleaf) as the main effect. As above, we selected α = 0.10 prior to performing the analysis because of relatively small sample sizes. All statistical tests were conducted using R version 3.5.3 (R Core Team 2018).

Results

Foliar CT concentrations were lower among trees in the Fremont zone (mean = 8.75 ± 0.401 mg/g, dry mass), than among trees in either the hybrid zone (134 ± 22.2 mg/g) or the narrowleaf zone (154 ± 18.2 mg/g), which is consistent with previous work along this *Populus* hybridization gradient (Schweitzer et al. 2004). Soil nitrification potential declined by ~75% with increasing foliar CT concentrations across the *Populus* hybridization gradient (Fig. 1a). The abundance of ammonia-oxidizing archaea also had a negative relationship with foliar CT concentrations, declining by ~66% across the *Populus* hybridization gradient (Fig. 1b). In contrast, stand-level foliar CT concentrations were not a significant predictor of soil bacterial *amoA* gene abundance (Fig. 1c). Other stand-level environmental factors known to influence nitrification, including soil moisture, soil pH, foliar N concentrations, soil organic C concentrations, soil total N concentrations, and soil C:N, were relatively constant across the *Populus* hybridization gradient (Table 1) and were not significant predictors of potential nitrification rates, archaeal *amoA*, or bacterial *amoA* ($P > 0.10$ in all cases).

The ratio of archaeal to bacterial *amoA* in the Fremont zone was ~60% higher than in either the hybrid or narrowleaf zones on average, but differences across zones were not statistically significant ($F = 1.24$, $P = 0.299$, df = 2, 50) because of high within-zone variability, especially within the hybrid zone (coefficient of variation = 168%). Archaeal *amoA* was more abundant than bacterial *amoA* in ~85% of the 54 individual soil samples taken across the nine *Populus* forest stands. Bacterial *amoA* gene abundance exceeded that of archaeal *amoA* in one soil sample from the Fremont zone, three soil samples from the hybrid zone, and four soil samples from the narrowleaf zone (*n* = 18 soil samples per zone).

DISCUSSION

Genetic variation in plants has become increasingly recognized as an organizing and predictive force governing the structure and function of terrestrial ecosystems. We used a naturally occurring *Populus* hybridization gradient to test the hypothesis that genetic variation in a heritable

plant trait, foliar CT concentrations, influences the activity and abundance of AOA and AOB, two phylogenetically distinct groups of soil autotrophic microorganisms that perform the first and rate-limiting step of nitrification, a key process regulating ecosystem N-retention. The decline in potential nitrification rates with increasing foliar CT concentrations across the *Populus* hybridization gradient is consistent with our hypothesis and with previous findings from both field and laboratory studies (Hattenschwiler and Vitousek 2000, Kraus et al. 2003, Schweitzer et al. 2008*b*). By measuring potential rates of nitrification in tandem with quantifying AOA and AOB *amoA* gene abundance, our results suggest that long-term inputs of foliar CTs may decrease the functional capacity of ammonia-oxidizing populations largely by reducing the abundance of AOA. These results further extend the influence of plant genetic variation on ecosystem processes, in this case nitrification, with the potential to feedback and affect both plant performance and ecosystem function. In addition, our results suggest for the first time that a heritable plant trait can influence the abundance of another group of autotrophic organisms, soil archaeal ammonia oxidizers, with no trophic linkage to plants as a source of carbon.

Extended effects of foliar CTs on nitrification

Although there is some evidence that CTs can directly inhibit nitrification (Kraus et al. 2003), we hypothesize that foliar CT inputs to soil indirectly reduce nitrification rates and AOA abundance by slowing rates of organic matter decomposition and net N mineralization. Condensed tannins reduce rates of decomposition and NH_3/NH_4^+ release presumably by forming complexes with both proteins from decomposing leaf litter and with extracellular enzymes
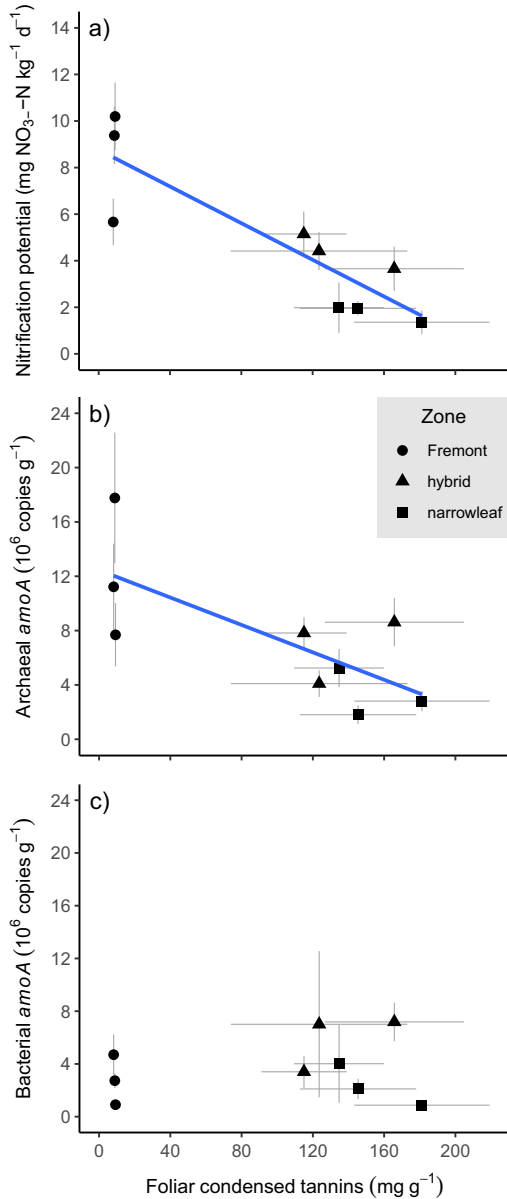

Fig. 1. Mean soil potential nitrification rates (a), mean soil gene abundance of archaeal *amoA* (b), and

(Fig. 1. *Continued*)
mean soil gene abundance of bacterial *amoA* (c) as a function of mean foliar condensed tannin concentrations of canopy trees in nine gallery forest stands across a naturally occurring *Populus* hybridization gradient. Horizontal and vertical error bars represent one standard error of the mean for each forest stand: $R^2 = 0.77$, $P = 0.002$ for (a); $R^2 = 0.53$, $P = 0.03$ for (b); $P = 0.61$ for (c); df = 7 for all three regressions.

Table 1. Biogeochemical characteristics of nine forest stands across a naturally occurring *Populus* hybridization gradient in northern Utah, USA.

Location	Foliar nitrogen (mg/g)	Soil pH	Soil organic carbon (g/kg)	Soil total nitrogen (g/kg)	Soil carbon to nitrogen mass ratio
Fremont zone					
Stand 1	21.0 (1.0)	7.29 (0.05)	40.9 (2.7)	2.0 (0.2)	21.13 (0.18)
Stand 2	18.4 (0.7)	7.21 (0.05)	28.7 (3.4)	1.5 (0.2)	19.61 (0.10)
Stand 3	18.1 (1.0)	7.35 (0.04)	39.0 (2.8)	1.9 (0.2)	21.07 (0.15)
Hybrid zone					
Stand 4	18.6 (0.5)	7.26 (0.06)	39.5 (8.8)	2.4 (0.6)	18.46 (0.79)
Stand 5	17.7 (1.0)	7.17 (0.04)	45.2 (7.0)	2.6 (0.4)	17.90 (0.08)
Stand 6	16.7 (0.8)	7.30 (0.02)	27.0 (4.1)	1.5 (0.2)	17.80 (0.26)
Narrowleaf zone					
Stand 7	16.2 (0.5)	7.24 (0.03)	81.1 (9.2)	4.2 (0.5)	19.59 (0.23)
Stand 8	18.1 (0.7)	7.21 (0.10)	20.4 (1.3)	0.7 (0.1)	31.05 (0.34)
Stand 9	19.0 (0.4)	7.30 (0.06)	30.7 (3.4)	1.2 (0.1)	26.47 (0.15)

Note: Values are means with standard error of the mean in parentheses ($n = 6$ per forest stand).

released into the soil solution by heterotrophic microorganisms (Hattenschwiler and Vitousek 2000), thereby reducing substrate supply to ammonia oxidizers. Previous work along the same *Populus* hybridization studied here demonstrated that increasing inputs of litterfall CTs to soil reduced annual rates of leaf litter decomposition, net N mineralization, and soil NH_3/NH_4^+ availability (Schweitzer et al. 2004, Fischer et al. 2010). Litterfall CT inputs to soil were also positively correlated with an increase in *Populus* fine root production, presumably to compensate for the decline in soil N availability (Fischer et al. 2006). In addition, several laboratory experiments have demonstrated that CTs from other plant species added to soil reduce rates of net N mineralization (Schimel et al. 1998, Fierer et al. 2001, Kraus et al. 2003). Taken together, this evidence suggests the long-lived and cascading influence of genetic variation in foliar CTs extends to nitrification, a key ecosystem process that regulates ecosystem N-retention. Because foliar CTs are heritable, they are subject to selection pressures, suggesting that different evolutionary trajectories of this plant trait within *Populus* species could alter the N status of entire ecosystems.

Contrasting differences in AOA and AOB responses

The discovery of ammonia oxidizers in the Thaumarchaeota has spurred an ongoing search for key environmental and physiological factors leading to niche specialization and differentiation of soil AOA and AOB (Taylor et al. 2012, Lu et al. 2015, Carey et al. 2016, Hink et al. 2018). Our results indicate that genetic variation in the foliar chemistry of a foundation tree species may be an important factor influencing this niche differentiation. The linear decline in potential nitrification rates mirrored the linear decline of AOA abundance with increasing foliar CT concentrations across the *Populus* hybridization gradient but there was no trend in AOB abundance, suggesting AOA played a dominant role in nitrification in these forest ecosystems. A potential caveat to this conclusion is that qPCR cannot distinguish between live, dead, or dormant (inactive) DNA. However, several studies have demonstrated that *amoA* gene abundance derived from qPCR varies in response to factors that also affect nitrification rates (Carey et al. 2016). Our results contrast with a recent meta-analysis showing that *amoA* gene abundance of AOB was more responsive to N additions than that of AOA, and that increased nitrification potential with N addition was only correlated with AOB (Carey et al. 2016). However, our study system differs from most of the studies included in the Carey et al. (2016) meta-analysis in two fundamental ways. First, changes in NH_3/NH_4^+ availability in Carey et al. (2016) were primarily from high rates of inorganic N addition, but were driven by declines in N derived from decaying organic matter induced by variation in foliar CT concentrations across the *Populus* hybridization gradient. Several lines of

evidence suggest that AOA are more responsive to N derived from organic matter mineralization than to inorganic N additions (Levičnik-Höfferle et al. 2012, Lu et al. 2015, Carey et al. 2016). Second, AOA are often the predominant contributors to nitrification in soils with neutral to slightly basic pH and low-to-moderate NH_3/NH_4^+ availability (Levičnik-Höfferle et al. 2012, Lu et al. 2015, Hink et al. 2018), as was the case in our study system. This evidence suggests that, although AOA appear better adapted to low-N ecosystems than AOB, their activity and abundance are still sensitive to heritable plant traits that reduce rates of N mineralization from organic matter.

Implications

Our results have several implications for research examining species interactions and the extended effects of plant genetic variation on the structure and functioning of terrestrial ecosystems. First, we have demonstrated that the biochemistry of a photoautotroph in one domain of life (Eukarya) can influence the abundance and activity of chemoautotrophs in another domain of life (Archaea). This linkage of phylogenetically and functionally distinct autotrophs indicates that species interactions are not limited to direct trophic interactions or even to trophic cascades, because both *Populus* trees and soil ammonia oxidizers independently fix carbon directly from the atmosphere. Second, although potential nitrification rates declined consistently with increasing foliar CT concentrations, the abundance of AOA and AOB responded very differently, suggesting a shift in competitive balance and possibly turnover of individual species of AOA and AOB in response to reductions in NH_3/NH_4^+ supply (Fischer et al. 2010). Finally, our results have implications for plant–soil feedbacks by providing further evidence that plants may actively control terrestrial N cycling (Chapman et al. 2006). The conversion of NH_3/NH_4^+ to NO_3^- via nitrification invariably leads to N losses from terrestrial ecosystems (Vitousek et al. 1982). Nitrate (NO_3^-) is highly mobile in the soil solution and thus easily lost from soils via leaching. Additionally, nitrification drives gaseous N losses to the atmosphere both directly and indirectly through denitrification that requires NO_3^- as a substrate. Our results provide further evidence that genetic predisposition toward high tannin production in *P. angustifolia*, F_1, and backcross hybrids may be adaptive by serving as a N-retention mechanism in N-limited environments (Fischer et al. 2006).

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DATA AVAILABILITY

All data and R scripts are available online at https://doi.org/10.5281/zenodo.2715740