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Root traits and rhizosphere processes reflect differential phosphorus acquisition strategies in contrasting *Populus* clones

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ABSTRACT

Soil phosphorus (P) availability and its distribution influence plant growth and productivity. To evaluate strategies that allow genotypes to be efficient under variable P environments, we planted six hybrid *Populus deltoides* clones belonging to the section *Aigeiros* (Aig), LL1, LL9, NL351, NL35, NL1388 and NL895, to three growth conditions in a greenhouse experiment, including low P, a high homogenous P supply and a high heterogeneous P supply. Functional traits, including foliar and root traits as well as rhizosphere processes, were measured. Large genotypic variation in shoot biomass and leaf P concentration was found in response to the P supply level and pattern. Compared with no P supply, LL1, LL9 and NL895 had a greater root length, biomass and P concentration in leaves under a homogenous P supply, while growth traits of NL351, NL35 and NL1388 were not significantly affected. A heterogeneous P supply enhanced the shoot biomass of LL1 and LL9. The root proliferation of LL1 and LL9 in P-rich patches was related to increased P acquisition in leaves. By contrast, a heterogeneous P supply did not enhance the biomass accumulation and the morphological plasticity of roots in other four genotypes, NL351, NL35, NL895 and NL1388, in P-rich patches. We found that functional traits or rhizosphere processes under low P could predict high P performance in *Populus* clones. Genotypes with a higher specific root length under low P can accumulate a larger biomass under a homogenous P supply. Conversely, high acid phosphatase concentrations decreased the positive impact of a heterogeneous P supply on a genotype's performance. Our results provide implications and applications for silviculture and forest management.

1. Introduction

Phosphorus (P) is pivotal for plant growth and metabolism. It participates in many important metabolic processes, including the production and synthesis of nucleic acids and membrane phospholipids. However, the availability of P in soil is relatively limited due to biochemical interactions with other minerals, such as free Fe or Al oxides (Ohno et al., 2007; Shen et al., 2011). Hence, P shortage is the main factor restricting plant growth and leading to yield reduction. In response, plants have developed highly specialized morphological root traits to enhance the soil exploration volume for P assimilation, such as increasing the specific root length (SRL), and density and length of lateral roots, as well as creating symbiotic relationships with mycorrhizal fungi (Fransen et al., 1998; Burleigh et al., 2002; Peret et al., 2011; Miguel et al., 2015). Additionally, plants can enhance P availability by mining P in the rhizosphere via the release of Pi-solubilizing root exudates, such as organic acids, enzymes and hydrogen protons, which can significantly enhance the rhizosphere soil Pi availability (Neumann and Martinoia, 2002; Lambers et al., 2009; Pang et al., 2018).

P distribution in forests is considered to be heterogeneous or patchy because of variation in physical and chemical properties of organic soil inputs and spatiotemporal variation in organic matter decomposition (Rodriguez et al., 2009). Trees exploit and utilize soil nutrient patches through root proliferation (Hodge, 2004; Wang et al., 2006). This is an effective strategy to adapt to spatiotemporal variability in P availability, often considered to be a compensatory response (Richardson et al., 2009; Yan et al., 2019). In this case, roots can acquire more nutrients in a heterogeneous environment than in a homogenous one, even though the total amount of available nutrients (including nitrogen, P or other mixed nutrients) is equal in both, leading to a greater plant biomass production and growth (Hutchings and Wijesinghe, 2008; Li et al., 2013; Zhang et al., 2017; Guo et al., 2019). However, responses to nutrient heterogeneity vary between and within tree species. In

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greenhouse conditions, N heterogeneity has been found to increase root proliferation and whole-plant growth in *Fraxinus pennsylvanica* but not in *Liquidambar styraciflua* or *Nyssa aquatica* (Gloser et al., 2008); growth and P uptake efficiency have been shown to vary among *Pinus massoniana* genotypes under both homogeneous and heterogenous P conditions (Zhang et al., 2012). It is thought that the extent of adaptive changes and the efficiency of foraging nutrients in response to soil P distribution are distinct among plant species and even among genotypes.

Functional traits can be used to explain the ability to adapt to abiotic stresses (Richardson et al., 2011; Fort et al., 2015; Balachowski et al., 2018; Pang et al., 2018). Previous studies have proposed that plants with thinner roots could be better adapted to both low and heterogeneous nutrient conditions (Mommer et al., 2011). Nevertheless, a specific root trait cannot accurately define P acquisition strategies under variable soil P (Zemunik et al., 2015; Ceulemans et al., 2017). In fact, the adaptation strategy of plants to low soil P is context-specific (Li et al., 2018). For instance, plants can capture available inorganic P via roots or mycorrhizal hyphae in soil either directly or by hydrolyzing organic P through which roots would increase their P acquisition (Shen et al., 2011; Wang et al., 2017). Fort et al. (2015) have suggested that strong trade-offs in soil P exploration strategies are found between conservative and acquisitive *Fabaceae* species. Acquisitive species depend on morphological root foraging, while the conservative species mineralize organic P through a higher phosphatase activity in rhizosphere soil. Chen et al. (2016) have conducted a field experiment to study how root traits drive nutrient acquisition strategies in nutrient patches. Their results indicated that tree species with thick roots construct absorptive roots at a higher cost than species with thin roots, and mycorrhizal fungi show more hyphae proliferation in nutrient-rich patches. In all, there are distinct P acquisition strategies, but our knowledge about how the diverse traits drive P acquisition strategies in various soil environments is still limited.

Populus clones display distinct growth characteristics and nutrient absorption efficiencies (Nelson et al., 2018; Niemczyk et al., 2018). They do not only show significant variation in dry matter production and nutrient uptake, but also possess considerable variation in P acquisition strategies (Gan et al., 2016; Wang et al., 2016). *P. deltoides* is an important tree species for timber production and soil restoration in China because of fast growth, outstanding disease resistance and strong environmental adaptability. The broad area from the south-side of the Yangtze River (25°N) to the south-side of the Heilongjiang province (53°N) is suitable for planting *P. deltoides*. The plantation area is more than 6 million hm^2. At the present, there are many *P. deltoides* clones that have been created through directional breeding (Gong et al., 2011; Yan et al., 2017). Because there is considerable soil P variation in China, it is necessary to explore the response and adaptation mechanism of specific genotypes to P deficiency and heterogeneous P distribution. Considering that the planting of *P. deltoides* should be adapted to local P conditions, we planted six *P. deltoides* strains under high and low soil P conditions. Among them, high P is divided, according to the supply pattern, into a homogenous and heterogeneous supply. By measuring a series of functional traits, rhizosphere processes, growth performance and P concentrations in leaves, we aimed to answer two following questions: (i) Is there genetic variation in the response of *P. deltoides* to P supply level and pattern? (ii) How do functional traits of different *P. deltoides* genotypes drive P acquisition strategies under variable soil P?

2. Materials and methods

2.1. Plant materials and soils

Healthy and uniform cuttings were taken from *P. deltoides* hybrids belonging to *Aigeiros* (Aig), obtained from the Shandong Academy of Forestry and Poplar Research and Development Center in Nanlin. The genotypes used were LL1 (*P. deltoides* × *P. deltoides*), LL9 (*P. deltoides* × *P. deltoides*), NL351 (*P. deltoides* × *P. deltoides*), NL35 (free pollination of *P. deltoides*), NL895 (*P. deltoides* × *P. euramericana*), and NL1388 (*P. deltoides* × *P. euramericana*). LL1 and LL9 are widely planted in the northern Shandong Peninsula, while NL 351, NL35, NL895 and NL1388 are southern *P. deltoides* clones, which are popular in the middle and lower reaches of the Yangtze River. One-year-old poplar sapling (3–4 m in height) stems were collected from basal positions in early March of 2018. Cuttings were approximately 18–20 cm in length and 2 cm in diameter with 2–4 dormant buds (see Wang et al., 2016). Previous studies suggested that spring was more appropriate time for hardwood cuttings (Zhao et al., 2014). Also, the position should be the base of the shoot (Zalesny et al., 2003). The cuttings were sealed in polyethylene bags and chilled for 14 d at 4 °C to promote uniform bud sprouting. Low P soil was collected randomly from barren land near the Hangzhou Normal University. The soil is sandy loam with pH 8.64, soil organic matter content of 2.82 g kg^{-1}, total N of 0.28 g kg^{-1}, Olsen-P of 2.62 mg kg^{-1} and available K of 90.65 mg kg^{-1}. Soil samples were air-dried and passed through a 2-mm sieve to remove plant tissues. The experiment was conducted in a glasshouse at the Hangzhou Normal University in Zhejiang. During the growth period, the temperature was kept at 21–25 °C during the day and at 15–18 °C during the night, with 12–14 h light in the glasshouse.

2.2. Experimental design and plant harvesting

In order to assess genotypic variation in how the availability and spatial distribution of P affect the performance of *P. deltoides*, we set up a completely randomized experiment comprising six different genotypes and three P treatments, with four replications in each treatment. The experiment was conducted using a specific root segregation device made of PVC material (length 20 cm × width 20 cm × height 30 cm), divided into two equal compartments by a rigid plastic wall. The partition in the middle prevented the exchange of nutrients between the compartments (Fig. S1). Each root device was equipped with 10 kg soil. A fine, 3-cm deep sand layer was placed on the top of the soil as a buffer zone to ensure natural root growth. The experiment comprised a total of 72 cuttings. Three P treatments were conducted with different P supply levels or patterns: (1) low-P, no P applied into soil; (2) high-P, P supplied in a heterogeneous pattern; (3) high-P, P supplied in a homogeneous pattern. P was added as $Ca(H_2PO_4)_2{\cdot}H_2O$ in both high P treatments with the same total amount of P. In the heterogeneous P treatment, 2 g of P was manually mixed into one side of the root box as a P-rich patch (402.6 P mg/kg soil), and the other side was not treated as the background soil (2.6 P mg/kg soil). In the homogeneous P treatment, 2 g of P was spread evenly throughout the soil of both compartments (202.6 P mg/kg soil). In order to ensure adequate plant growth, other nutrients were uniformly applied to soil (mg per pot): $Ca(NO_3)_2{\cdot}4H_2O$ 8040; K_2SO_4 100; $MgSO_4{\cdot}7H_2O$ 130; $MnSO_4{\cdot}H_2O$ 50; $ZnSO_4{\cdot}7H_2O$ 75; $CuSO_4{\cdot}5H_2O$ 15. One cutting of *P. deltoides* from each genotype was planted at the center of each root segregation device (Northwest Agricultural University and South China Agricultural University, 1992). Pots were watered (about 35% field capacity) every two days throughout the experiment.

Cuttings were planted in late March of 2018, harvested in August (growth for 20 weeks), and divided into leaves, stems and roots prior to further processing and measurements. Here, in order to select functional traits under low P to predict genotypic performance under homogeneous P or heterogeneous P applications, foliar and root traits as well as related rhizosphere processes were measured for the low P treatment. These traits would be useful to develop appropriate forestry fertilization strategies in infertile soils.

2.3. Foliar trait measurements

One week prior to the final harvest, the photosynthetic

characteristics were measured in low-P treatments for the third or fourth expanded and intact leaf with a portable photosynthesis system (LI-6400; Li-Cor Inc., Lincoln, NE, USA) between 08:00 and 11:30 h. Net photosynthetic rate (Pn, μmol m^{-2} s^{-1}), stomatal conductance (Gs, mol m^{-2} s^{-1}) and transpiration rate (E, mmol m^{-2} s^{-1}) were calculated under the following conditions: the air flow rate chamber was 500 μmol s^{-1} through the sample, and the leaf temperature was kept at 25 ± 0.8 °C. The CO_2 concentration of the chamber was adjusted to 400 ± 5 μmol mol^{-1}. The leaves chosen for photosynthesis parameters were measured as the one-side area of a fresh leaf per cutting, scanned at 400 dpi resolution, and analyzed using Image J software. Subsequently, the specific leaf area (SLA, cm^2 g^{-1}) was calculated by the ratio of the one-side area divided by its oven-dried mass (Perez-Harguindeguy et al., 2013). Also, leaf thickness (LT, mm) was measured using an electronic apparatus (YH-1; Topper Instruments Corporation, Zhejiang, China) for transverse sections at the intermediate point between the border of the leaf and the midrib, avoiding secondary veins. The leaf tissue density (LTD, g cm^{-3}) was defined as leaf mass/(leaf area × leaf thickness).

2.4. Root trait measurements

In low P treatments, all roots were gently picked out from soil and washed in deionized water. A part of the roots (15–30 pieces of 15-mm long fine root segments per plant) from each plant was excised from the root system, then analyzed for the arbuscular mycorrhizal fungi (AMF) colonization rate, as described by Vierheilig et al. (1998). Roots segments (15 mm long) were randomly sampled from each treatment, washed in distilled water, and then immersed in a FAA fixative for 4 h. Root segments were bleached in 10% KOH for 1 h and stained in ink and vinegar (95% vinegar and 5% ink) for 3 min at 90 C. All stained root segments were randomly selected for microscopic observations to calculate the colonization rate (Col%). Then, the coarse roots (> 2 mm) were separated from fine roots and scanned with a desktop scanner at 400 dpi (Epson Expression1600, Japan). The total root length and root volume (including both coarse and fine roots) were analyzed by the Win-RHIZO software (WinRhizo Pro2004b, version 5.0, Regent Instruments Inc., Canada). The coarse root percentage (CR%) was calculated as the percentage of the coarse root length of the total root length. After that, the harvested roots were dried at 75 °C for 72 h and weighed to calculate specific root length (SRL, m g^{-1}) and root tissue density (RTD, g cm^{-3}). SRL and RTD were calculated by dividing the sample root length by its dry mass and as the ratio of the sample root dry mass to its volume, respectively. Also, root length density (RLD, cm cm^{-3}) was calculated by dividing the sample root length by its growth volume.

2.5. Determination of rhizosphere processes

After root excavation, rhizosphere soil (soil adhering to fine roots) was sub-sampled for the pH and acid phosphatase as well as for carboxylate measurements. The pH of the rhizosphere soil was measured using a pH meter (the ratio of soil to $CaCl_2$ solution was 1:2.5). The soil acid phosphatase (ACP) activity was analyzed according to Neumann (2006): briefly, 0.5 g rhizosphere soil was homogenized (2 ml deionized water, 0.4 ml acetate buffer (pH 5.2) and 0.1 ml substrate [pNPP (p-nitrophenylphosphate); Sigma-Aldrich. USA). Followed by gentle shaking and incubation for 30 min at 30 °C, the reaction was stopped with 0.5 ml 0.5 M NaOH, and the homogenate was centrifuged at 12,000 × *g* for 10 min. For the controls, NaOH was added before incubation. The absorbance was measured with a spectrophotometer at 405 nm. The quantification of carboxylates was performed by high-performance liquid chromatography (HPLC) (Zhang et al., 2016). In short, 5 g rhizosphere soil was transferred to a vial containing 50 ml of 0.2 M $CaCl_2$ and carefully shaken to dislodge the rhizosphere soil, followed by shaking for 5–10 s to form a homogenate. A suspension volume of 10 ml was filtrated and transferred to a 10-ml centrifuge tube and then loaded onto a 250 × 4.6 mm reversed-phase column (Alltima C18, 5 μm, USA), which was equilibrated with 25 mM KH_2PO_4 (pH 2.25) with a constant flow rate of 1 ml min^{-1} at a temperature of 31 °C. Carboxylates were detected at 214 nm with a diode array UV detector.

2.6. Shoot biomass, phosphorus uptake and P response indexes

The shoots were oven-dried at 75 °C for 72 h. Afterwards, leaves were weighed and homogenized for P concentration measurements (Johnson and Ulrich, 1959). To evaluate the effect of P on the genotypic performance, we calculated P response indexes that depend on dry matter accumulation for each genotype: Response index to P supply level = $(P_H - P_L)/P_L$, where P_H is the mean dry matter of shoots grown with a high and homogeneous P supply and P_L is the dry matter of shoots grown with no P addition. Response index to P supply pattern = $(P_{Hetero} - P_{Homo})/P_{Homo}$, where P_{Hetero} is the mean dry matter of shoots of genotypes grown with a heterogeneous P supply and P_{Homo} is the mean dry matter of shoots of genotypes grown with a homogeneous P supply. The higher the index, the larger the effect of the P supply level or heterogeneous P supply.

2.7. Data analysis

Tukey's Honestly Significant Difference (HSD) tests after one-way analyses of variance (ANOVAs) were used to compare individual differences among means at a significance level of $P < 0.05$. Differences in the shoot biomass and foliar P concentration between P supply levels and patterns of specific genotypes were identified by independent-samples *t*-test. The effects of genotypes, P treatments and their interactions were tested by two-way ANOVAs, when ANOVA terms were significant using SPSS 16.0 for Windows (SPSS Inc. Chicago, Illinois, USA). The ability of plant functional traits and rhizosphere processes (predictor variables) to explain the performance of genotypes (response variables) was tested using generalized linear models (GLMs), followed by a stepwise Akaike's information criterion (AIC) approach. We screened crucial predictor variables to significantly improve the prediction of response variables. The reliability of functional traits and rhizosphere parameters to predict shoot biomass accumulation or P response indexes were analyzed separately under each growth condition. To characterize associations between growth responses to variable soil P, crucial functional traits and rhizosphere parameters, we calculated Pearson's correlation coefficients for each genotype using individual data.

3. Results

3.1. Passimilation and the performance of genotypes

T-test analyses showed that there were genotype-specific responses in shoot biomass and leaf P concentrations to the P supply level and pattern (Table S1). The P supply level significantly influenced the shoot biomass and P concentrations of LL1, LL9, NL351 and NL895, while the P supply pattern affected the shoot biomass and leaf P concentrations of LL1, LL9. However, the shoot biomass and P concentrations of NL35 and NL1388 were unaffected by the P supply level and pattern. Furthermore, large differences were found between genotypes' shoot biomass production among treatments (Table 1). Three genotypes, LL1, LL9 and NL895, showed outstanding growth when compared to other genotypes under all growth conditions; they were particularly efficient in dry matter accumulation under high P. On the other hand, a heterogeneous P supply stimulated the shoot growth of LL1 and LL9 more than a homogeneous supply (Table 1). The other two genotypes, NL351 and NL35, also showed positive responses to high P under a heterogeneous P supply, but the promoting effect was not significant. The dry matter of NL1388 was lowest under high P but it was influenced less by low P. However, a heterogeneous P supply did not induce a positive

Table 1
Shoot biomass (mean ± SE, n = 4) and P response indexes of six *P. deltoides* genotypes under three different P conditions.

Genotype	Shoot biomass (g)			Response index of	
	Low P	High P			
		Homogeneous	Heterogeneous	P level	P pattern
LL1	25.19 ± 1.66aC	41.66 ± 2.62aB	54.20 ± 1.30aA	0.65	0.23
LL9	22.45 ± 1.75abC	43.14 ± 3.03aB	60.34 ± 3.00aA	0.92	0.28
NL351	15.65 ± 0.57cB	19.48 ± 0.61bAB	22.44 ± 2.77bcA	0.25	0.13
NL35	16.80 ± 1.18bcA	22.95 ± 3.25bA	25.92 ± 3.32cdA	0.36	0.11
NL1388	14.59 ± 0.49cA	17.40 ± 0.32bA	16.08 ± 1.38dA	0.19	−0.08
NL895	17.37 ± 1.53bcB	37.40 ± 3.36aA	46.76 ± 3.18abA	1.15	0.20

Different letters indicate significant differences within a column (lower case) or row (ANOVA and post hoc Tukey's HSD test) (upper case).

effect on the growth of NL1388.

P application and genotype significantly affected the foliar P concentration of *Populus* clones. P application significantly increased the leaf P concentrations of LL1, LL9 and NL895, but not that of NL35 and NL1388 (Fig. 1). Also, genetic differences in leaf P concentrations were found between the two P supply patterns. When soil P was applied heterogeneously, the leaf P concentrations of LL1 and LL9 were higher than those under a homogeneous application, whereas other genotypes did not show significant differences between responses to two P application patterns.

3.2. Root morphology

Genotypic variation affected the root/shoot ratio and total root length of *Populus* clones, while they were unaffected by P supply levels and patterns (Fig. 2a, b). Low P largely increased the root/shoot ratio of LL1, LL9, NL351 and NL895, but not that of NL35 and NL1388. However, none of the genotypes showed significant variation between homogeneous and heterogeneous P supply patterns. Genotypes LL1, LL9 and NL895 showed more significant responses to the P supply level in the total root length compared with NL351, NL35 and NL1388 (Fig. 2b). Moreover, the total root length of LL9 and NL895 were significantly greater under a heterogeneous P supply compared with a homogeneous one.

Genotypic variation affected root length density (RLD) outside and inside a P-rich patch, while P supply levels and patterns did not have any significant impact on RLD of *Populus* clones (Fig. 3a and b). For instance, compared with no P addition, a homogeneous P supply significantly increased RLD outside the P-rich patch in LL1 and LL9, but no significant effect was found in NL351, NL35, NL1388 and NL895. In addition, RLD outside the P-rich patch in six genotypes did not differ between P supply patterns. By contrast, RLD in the P-rich patch of LL9 and NL895 significantly increased from no P addition to a homogeneous P supply, but RLD of LL1, NL351, NL35, NL1388 was not

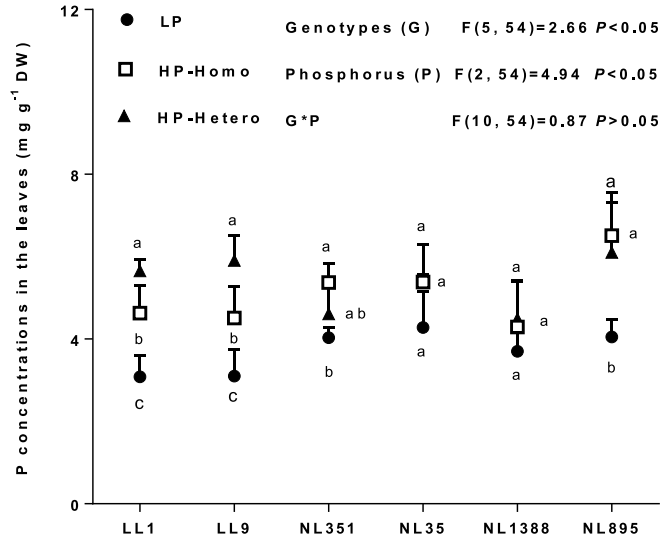

Fig. 1. Effects of P supply level and pattern on the foliar P concentration of six *P. deltoides* genotypes. Error bars, ± SE (n = 4). Columns with the same letter are not significantly different at $P < 0.05$ according to ANOVA, followed by Tukey HSD tests.

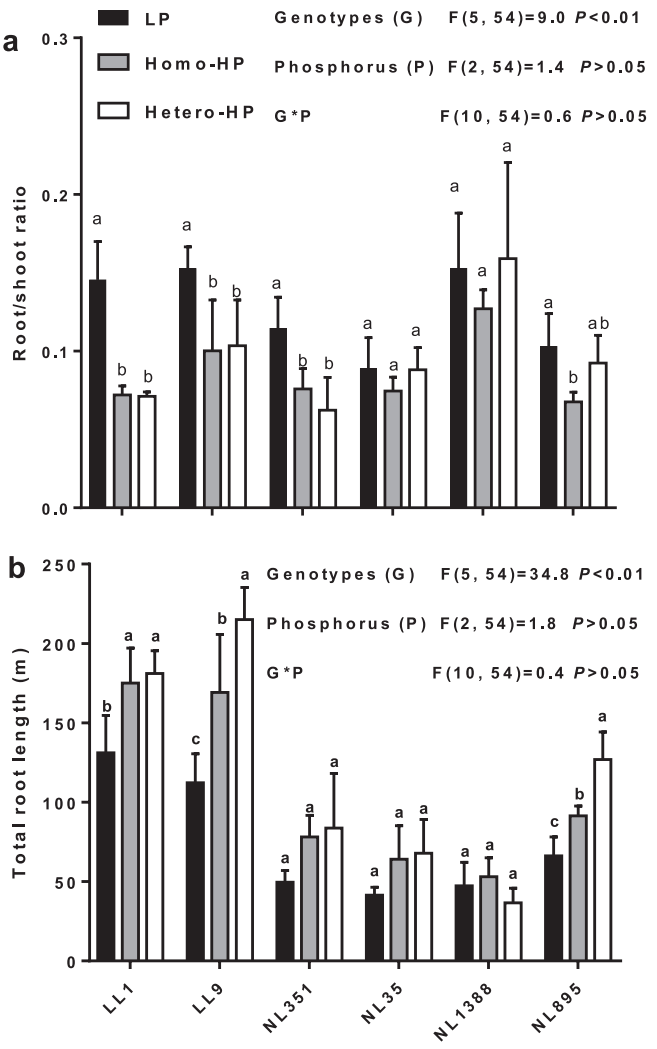

Fig. 2. Effects of P supply level and pattern on the root/shoot ratio (a) and total root length (b) of six *P. deltoides* genotypes. Error bars, ± SE (n = 4). Columns with the same letter are not significantly different at $P < 0.05$ according to ANOVA, followed by Tukey HSD tests.

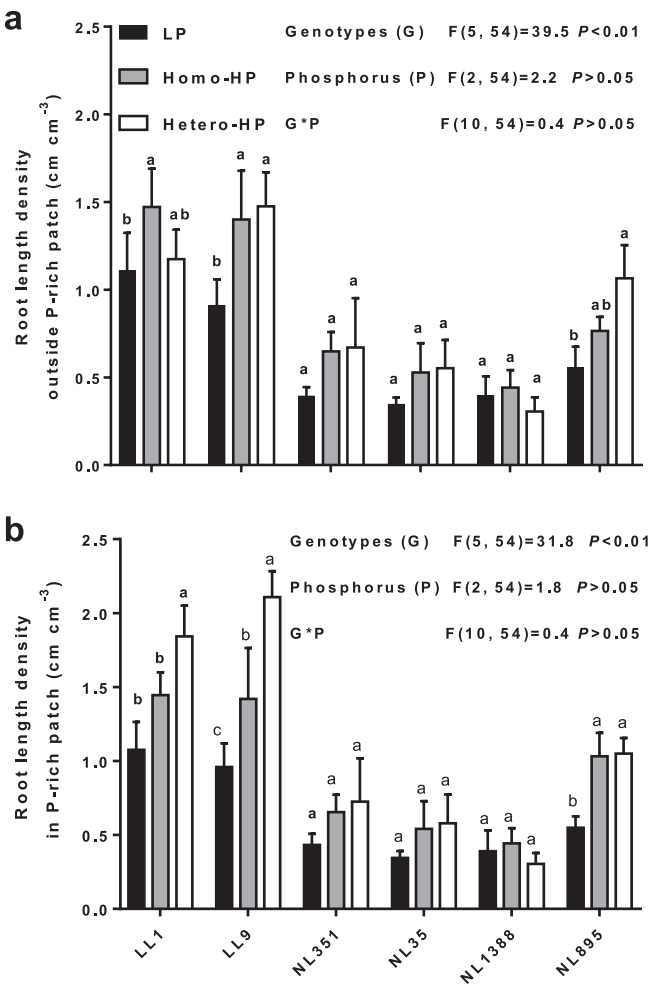

Fig. 3. Effects of P supply level and pattern on the root length density of *P. deltoides* clones outside (a) and within P enriched soil (b). We refer to high P zone in heterogeneous treatments as "P-rich soil" and the remaining soil without P additions as "outside P-rich soil". In homogeneous P treatments, corresponding positions are the same. Error bars, ± SE (n = 4). Columns with the same letter are not significantly different at $P < 0.05$ according to ANOVA, followed by Tukey HSD tests.

affected. Moreover, when P was supplied heterogeneously, RLD was higher in the P-rich patch of LL1 and LL9 compared with the homogeneous P application, while other four genotypes did not show significant differences between P supply patterns.

3.3. Rhizosphere processes and AMF dependence

Compared with other genotypes, NL1388 exhibited lower SRL but higher CR%, RTD, ACP and TC (Table 2). In addition, the carboxylate composition was significantly different among genotypes. Citrate was mostly found in the rhizosphere in all genotypes (on average, over 95% of the total amount) (Fig. S2). LL1 was the only genotype that exuded four types of carboxylates, whereas LL9, NL351 and NL895 exuded three types (oxalate, succinate and citrate) into the rhizosphere. In contrast, only two kinds of low-weight organic acids could be detected in the rhizosphere of NL35 and NL1388. Surprisingly, colonization rates by AMF don't vary with clones in the low-P treatment (Table 2).

3.4. Biomass production and P response indexes

Functional traits measured for each genotype grown under low P explain dry matter accumulation under different growth conditions as well as the response indexes of P supply level and pattern. GLM performed by the stepwise AIC procedure validly predicted genotypic performances, with R^2 of 0.96 for shoot biomass accumulation under a homogeneous P supply and 0.63 for the response index of P supply level (Table 3). LT, SRL and ACP were the three major factors associated with the dry matter accumulation. Finally, a significantly positive relationship was found between SRL in low P soils and the response index of P supply level ($R^2 = 0.71$, $P < 0.05$), while ACP in low P soils appeared negatively related to the response index of P supply pattern ($R^2 = 0.93$, $P < 0.01$) (Fig. 4a, b).

4. Discussion

4.1. Morphological plasticity among Populus clones responds to P supply level and pattern

Poplar productivity across a regional scale largely depends on interactions between genotypes and environments (Zalesny et al., 2009). Soil P is an important factor limiting poplar growth. Booth (2008) proposed that a single application of P fertilizer was superior to a single

Table 2
Trait values (mean ± SE, n = 4) of six *P. deltoides* genotypes grown under low P.

Plant traits	LL1	LL9	Genotypes NL351	NL35	NL1388	NL895
Foliar traits						
Leaf thickness (LT, mm)	0.19 ± 0.01b	0.17 ± 0.01ab	0.15 ± 0.01b	0.15 ± 0.01a	0.15 ± 0.01b	0.15 ± 0.01b
Leaf tissue density (LTD, g cm^{-3})	1.51 ± 0.05c	1.99 ± 0.13 cd	2.13 ± 0.10c	2.41 ± 0.14bc	2.94 ± 0.12a	2.83 ± 0.14ab
Specific leaf area (SLA, cm^2 g^{-1})	347.98 ± 10.20a	299.42 ± 11.93b	317.24 ± 7.95ab	277.83 ± 13.03b	230.06 ± 7.38c	229.47 ± 6.48c
Transpiration rate (E, mmol m^{-2} s^{-1})	5.04 ± 1.03a	5.22 ± 1.00a	5.18 ± 0.55a	4.85 ± 0.77a	6.75 ± 0.29a	3.99 ± 0.79a
Net photosynthetic rate (Pn μmol m^{-2} s^{-1})	17.00 ± 1.59a	16.09 ± 1.91a	15.96 ± 1.15a	16.15 ± 1.13a	12.54 ± 1.66a	13.98 ± 0.66a
Stomatal conductance (G_s, mol m^{-2} s^{-1})	0.45 ± 0.05a	0.36 ± 0.12a	0.38 ± 0.06a	0.35 ± 0.07a	0.52 ± 0.04a	0.28 ± 0.06a
Root traits						
Coarse root (CR%)	7.30 ± 0.45b	8.57 ± 1b	12.87 ± 2.8b	11.28 ± 0.51b	19.29 ± 0.82a	7.51 ± 0.92b
Specific root length (SRL, m g^{-1})	36.42 ± 3.32a	33.19 ± 2.95ab	28.31 ± 3.23ab	29.87 ± 4.87ab	20.89 ± 1.50b	37.9 ± 2.93a
Root tissue density (RTD, g cm^{-3})	0.19 ± 0.02c	0.24 ± 0.02bc	0.34 ± 0.04ab	0.28 ± 0.04bc	0.50 ± 0.04a	0.23 ± 0.01bc
Colonization rate (Col%)	29.5 ± 2.25a	27.25 ± 0.03a	31.00 ± 1.29a	30.00 ± 2.04a	28.00 ± 1.58a	30.25 ± 0.48a
Rhizosphere processes						
pH	7.57 ± 0.04a	7.65 ± 0.03a	7.62 ± 0.01a	7.60 ± 0.04a	7.58 ± 0.06a	7.52 ± 0.03a
Acid phosphatases activity (ACP, pNP μg h^{-1} g^{-1} soil)	24.55 ± 2.18b	21.22 ± 1.05b	34.36 ± 3.68ab	29.14 ± 1.02b	45.07 ± 5.24a	24.57 ± 2.26b
Total carboxylates (TC, μg g^{-1} soil)	184.98 ± 62.07c	291.91 ± 2.35bc	320.07 ± 22.25b	287.29 ± 2.57bc	738.11 ± 64.38a	284.53 ± 2.60bc

Columns with the same letter are not significantly different at $P < 0.05$ according to ANOVA, followed by Tukey HSD tests.

Table 3
Best-fit generalized linear models (intercept, linear predictor coefficients and significance) selected for total biomass and index of stress intensity, explained by plant functional trait values in response to different stresses. Full trait names are given in Table 2, AIC: Akaike's information criterion.

	Shoot biomass						Response Index			
	Low P		High P- Homogeneous		High P-Heterogeneous		P level		P pattern	
	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Intercept	−5.16	< 0.05	65.23	< 0.01	93.52	< 0.001			0.56	< 0.01
Foliar traits										
LT	185.22	< 0.001								
Root traits										
SRL							0.05	< 0.01		
Rhizosphere processes										
ACP	−0.20	< 0.01	−1.17	< 0.05	−1.88	< 0.05			−0.01	< 0.01
	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2
	−3.96	0.99	12.25	0.96	30.74	0.73	−13.83	0.63	−32.38	0.92

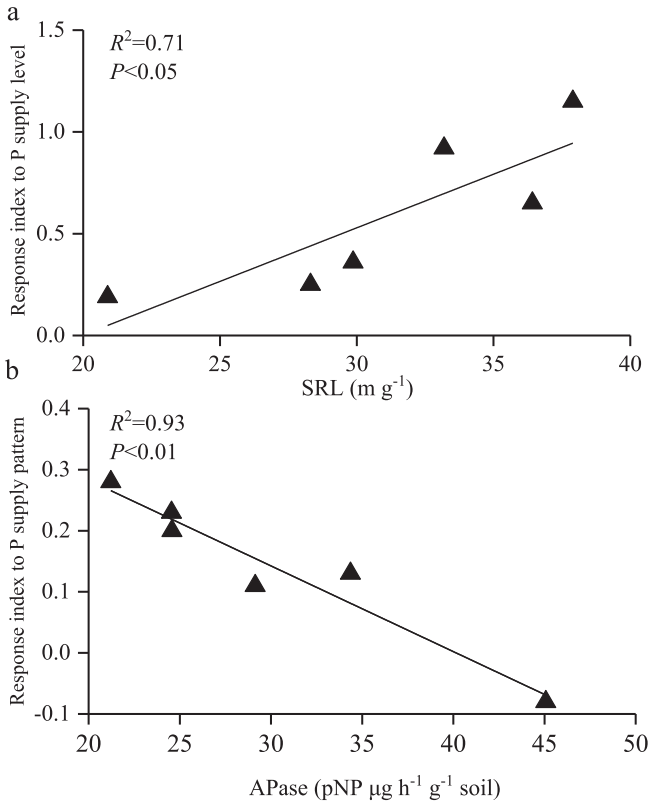

Fig. 4. Pearson's correlations among different traits in low P soils and P response indexes in six *P. deltoides* genotypes.

application of N fertilizer during the first growing season of hybrid poplars. Brown and Driessche (2002) also proved that the growth of poplar height and diameter was significantly correlated with the P content of leaves. However, fertilization does not necessarily increase the biomass production of poplars, and it depends on the genotype identity (DesRochers et al., 2006; Bilodeau-Gauthier et al., 2011; Amichev and Van Rees, 2018). In this study, we also found that the responses of *P. deltoides* to variable P strength and distribution differ among genotypes. The clones LL1, LL9 and NL895 are strongly dependent on an external P application to maximize growth. Contrastingly, the growth of NL1388 showed less sensitivity to the P supply level and pattern.

The root system plays a key role in nutrient absorption including Pi acquisition from the soil. Many previous studies have reported that root responses to nutrient application are dependent on root functional traits of the species (Bayuelo-Jimenez et al., 2011; Wu et al., 2011; Lyu et al., 2016; Huang et al., 2017). Particularly, trees with greater specific root length often possess more absorptive roots leading to a stronger capacity for nutrient acquisition, which can facilitate nutritional foraging under high nutrient supply conditions (Chen et al., 2018; Xia et al., 2019). In our study, clones LL1, LL9 and NL895 significantly increased the production of absorptive roots, which allowed more effective capture for added P and, consequently, greater increases in shoot biomass, even as they decreased their root/shoot ratio. By contrast, NL351, NL35 and NL1388 clones had a lower ability to proliferate roots under a high P environment. They used less of the added P, resulting in poor root growth (lower SRL but higher RTD).

Root morphology traits and their distribution in soil affect plant P acquisition (Chen et al., 2016; Xia et al., 2019). Numerous studies have shown that when soil P is heterogeneous, tree species and even different genotypes are plastic in their root morphology and increase numbers of lateral roots and growth of absorbing roots in P-rich patches (Zhang et al., 2012, 2017; Zhou et al., 2017; Farooq et al., 2018; Xia et al., 2019). These changes can enhance the foraging ability for P and adaptation to heterogeneously distributed P. Here, LL1 and LL9 relied on intensive root proliferation in P-rich patches, thereby having a greater opportunity for nutrient acquisition, while the root growth of NL35, NL351, NL1388 and NL895 showed less response to P supply patterns, resulting in a lower biomass accumulation in a highly heterogeneous P environment. Taken together, we found that *Populus* clones adopt different acquisition strategies in response to P supply patterns. Variation in the foliar P content and root growth with contrasting root morphological traits among genotypes confirmed the significance of root adjustments for P acquisition in a heterogeneous environment.

4.2. Adaptation of Populus clones to low P soils

Besides changes in root morphology, physiological and biochemical adaptation involves increased external P accqustion via enhanced rhizospheric processes (Shen et al., 2011; Huang et al., 2017; Pang et al., 2018). Plants can mediate the release of ACP and carboxylate from the roots to free Pi from phosphorylated compounds under acclimation to P shortage (Ceulemans et al., 2017). The induction of ACP has been reported in trees under a low P availability (Gan et al., 2016; Chen et al., 2018). Also, Desai et al. (2014) found that the exudation of organic acids by aspen (*P. tremuloides*) roots increased in response to P limitation. In our study, the ACP activity and carboxylate content in the rhizosphere of *Populus* clones were genotype-specific under low P conditions. NL1388 acquired soil P through an intensive exudation of carboxylates and ACP may have enhanced P mobilization and

acquisition. This may aid P acquisition by NL1388 in low-P soils, thus being less impacted by P shortage. In addition, its growth did not increase with added P. In contrast, other genotypes, especially LL1, LL9 and NL895, which are less dependent on the exudation of carboxylates and ACP in low P environments, showed a more positive response to the applied P through the extension of root absorption surface area to enhance spatial P availability. Thus, *Populus* genotypes may vary the relative importance of root growth and root exudation for P acquisition in low P soils.

4.3. Using root functional traits under low P to predict high P performance of Populus clones

Pearson correlations suggested that differences in belowground functional traits resulted in distinct performance under variable P. Thus, root traits and relevant rhizosphere processes potentially drive different P acquisition strategies among genotypes. In fact, both morphological and physiological strategies have considerable C costs, and plants may increase the expression of one mechanism at the expense of the other (Ryan et al., 2012; Huang et al., 2017). When the costs of the root system construction are relatively high under low P, as especially in genotypes with low SRL but high RTD, the plants may rely less on enhancing P absorption through root proliferation but more on mining or liberating P around roots through a physiological mechanism. This would be an economic strategy, because the cost of C spent on increased metabolic rates is less than that on constructing more roots (Le Roux et al., 2009; Funayama-Noguchi et al., 2015). Conservative genotypes with strong rhizosphere processes will be better able to tolerate low P stress (Lambers et al., 2008; Fort et al., 2015), but their limited root foraging ability with fewer lateral roots and a smaller total root surface area leads to lower chances to be in contact with soil P (Chen et al., 2018).

On the other hand, species with low SRL but high RTD can better resist herbivore and pathogen attacks, which may be beneficial in infertile soils (Laliberte et al., 2015). Thus, we propose that this may be another reason for NL1388 being less impacted by P shortage. In contrast, LL1, LL9 and NL895 produce thin and long roots (high SRL) with a relatively low carbon cost. Consequently, these clones may not need to extensively explore the soil around their roots, but rather build longer roots when compared to NL1388 with a similar C budget. Genotypes with high SRL absorb more P and are better able to adapt to high or heterogeneous P environments, resulting in greater growth benefits. However, this strategy may result in long-term costs and shorter lifespans of fine roots, which would not allow good adaptation to infertile soils in a long term (Freschet et al., 2018). It is noteworthy that besides relying on modifications in root morphology or physiology, *Populus* can also create symbiotic relationship with mycorrhizal fungi to enhance P absorption (Plassard and Dell, 2010; Ciadamidaro et al., 2017). However, in our study, there was no difference in colonization rates of AMF among different *Populus* genotypes in low P soils. Indeed, evolutionary asymmetry was discovered in the plant-mycorrhizal symbiosis, and a high degree of independence was found between mycorrhizal traits and plant performance (Koch et al., 2017). Van der Heijden et al. (2015) have also indicated that the morphological traits of AM fungi cannot predict host plant growth. Thus, the degree of AMF colonization rate could not predict the performance of *Populus* clones in high P soils. Taken together, important genotype × soil P interactions should be considered when breeding *Populus*, and specific genotypes should be planted according to local P conditions. Otherwise, less P fertilizer should be applied to NL1388, which can basically maintain its growth through physiological adjustment, while a local application of P fertilizer should be used to increase spatial P heterogeneity in the soils of LL1 and LL9, thereby improving the utilization efficiency of P and stand productivity through enhanced morphological plasticity of roots.

5. Conclusions

The present study showed that a functional strategy could be employed to balance morphological or physiological traits of roots in *Populus* in order to acquire P. The genotypes depending on morphological root foraging have a significantly positive response in high or heterogeneous P environments. In contrast, the genotypes with conservative physiological strategies are better able to tolerate P deficiency. Furthermore, diverse root characteristics and rhizosphere processes, such as SRL, RTD, CR(%), TC and ACP, are crucial for *Populus* clones for adopting suitable strategies in variable P environments. This knowledge is important when attempting to manipulate root morphology or rhizosphere processes in a specific clonal genotype to improve their P acquisition efficiency and to enhance the productivity of *Populus* plantations. Better understanding of strategies that promote growth will also aid genotypic selection of poplars adapted to local conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Zhichao Xia coordinated the research and wrote the manuscript, Yue He, Lei Yu and Jie Miao conducted the experiments, Helena Korpelainen contributed to the interpretation of data, manuscript preparation and revision, and Chunyang Li (the corresponding author) had the overall responsibility for the experimental design and project management.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117750.

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