



Light intensity influence maize adaptation to low P stress by altering root morphology

Tao Zhou · Li Wang · Xin Sun · Xiaochun Wang · Yinglong Chen · Zed Rengel · Weiguo Liu · Wenyu Yang

Received: 5 March 2019 / Accepted: 11 August 2019 / Published online: 22 August 2019
© Springer Nature Switzerland AG 2019

Abstract

Background and aims Soil phosphorus (P) availability, as well as shoot P status, may alter root morphology. However, how root morphological traits to light intensity under various P environments remains unknown. **Methods** Maize (*Zea mays* L.) cultivar CD418 grew under nine P application rates (ranged from 0 to 300 mg P kg⁻¹ soil, supplied as KH₂PO₄) under natural light intensity (NL) and low light intensity (LL, 40% of natural light intensity) in a naturally-lit rain-shed. Plant growth, P uptake, and responses of root morphological

traits (i.e. total root length, root surface area, and proportion of <0.2 mm diameter fine root) in the light and P treatments were assessed after 36 d of growth (five-leaf stage).

Results Shoot and root dry weights increased under the natural light intensity in all P treatments. The ratio of root to shoot dry weight increased under NL when the soil Olsen-P was below 15.9 mg kg⁻¹. At relatively low soil P availability (6.7 to 15.9 mg kg⁻¹), total root length, root surface area, and fine root percentage were enhanced with increases in light intensity from LL to NL. These effects diminished in soil with either severely low P (2.6 mg kg⁻¹) or excess P (above 20.6 mg kg⁻¹). Express of the low P-tolerance transcription factor *ZmPTF1* (that influences root growth by regulating carbon metabolism in leaves and roots), P uptake, and fertilizer P use efficiency were higher under NL than LL, especially under low P conditions (Olsen-P 6.7–15.9 mg kg⁻¹). Increased responses of root morphological traits to low P conditions were associated with relatively low P concentrations in the leaves and high sucrose concentrations in the roots.

Conclusions Compared to LL, under P deficiency and NL conditions, maize allocated more photosynthates to roots as sucrose, which acts as a low-P signal; in addition, sucrose as a carbon and energy source stimulated root growth and, consequently, adaptation of maize to low P stress.

Tao Zhou and Li Wang contributed equally to this work.

Responsible Editor: Jhonathan Ephrath.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11104-019-04259-8>) contains supplementary material, which is available to authorized users.

T. Zhou · L. Wang · X. Sun · X. Wang · W. Liu (✉) · W. Yang (✉)
College of Agronomy, Sichuan Agricultural University,
Chengdu 611130 Sichuan, China
e-mail: lwgsy@126.com
e-mail: mssiyangwy@sicau.edu.cn

T. Zhou · Y. Chen · Z. Rengel
The UWA Institute of Agriculture, School of Agriculture and
Environment, The University of Western Australia, Crawley, WA
6009, Australia

Y. Chen
Institute of Soil and Water Conservation, Northwest A&F
University, and Chinese Academy of Sciences, Yangling 712100
Shanxi, China

Keywords Photosynthesis · Root morphology · Phosphorus deficiency · Sucrose · Maize

Introduction

Phosphorus (P) is one of the most growth-limiting nutrients in plants (Vance et al. 2003; Vitousek et al. 2010). Studies reveal that crops take up only 10–25% of the fertilizer P applied each season (Johnston et al. 2014), and the rest of the fertilizer P is strongly bound to soil particles (Hinsinger 2001; Shen et al. 2011). Roots grown in soil with low P availability showed high plasticity to enhance the capacity of P acquisition, including morphological and physiological changes (Vance et al. 2003; Lambers et al. 2006; Shen et al. 2011). Increased photosynthates allocation to root growth, enhanced lateral root emergence, and increased production of fine roots, are the typical morphological responses that enlarge the contact area between roots and soil (Wang et al. 2010; Lambers et al. 2011; Niu et al. 2012; Postma et al. 2014; Lynch 2015). In addition, increased proton release, and higher exudation of carboxylates and phosphatases secretion into the rhizosphere may alter soil properties and release soil-bound P (Li et al. 2007; Richardson et al. 2011; Li et al. 2014; Mehra et al. 2016).

Many studies have investigated the contribution of root morphological and physiological changes to increased P acquisition in the environments with low P availability (e.g. Pang et al. 2009; Wang et al. 2010; Deng et al. 2014; Lyu et al. 2016; Li et al. 2016a). However, less attention has been paid to understanding how the aboveground light influences these adaptations in root morphology and physiology. Light intensity influence photosynthesis, the translocation of photosynthates to roots, and thus the growth and morphology of the root system (Hermans et al. 2006; Hammond and White 2008, 2011). The accumulation of root biomass and total root length are enhanced when plants are grown under high light intensity (Wissuwa et al. 2005; Cheng et al. 2014; Zhou et al. 2019). In contrast, root growth is more sensitive in reduction than shoot under low light intensity, resulting in decreased root to shoot biomass ratio, as the photosynthates are distributed preferentially to shoots during leaf extension to increase the interception of light (Hébert et al. 2001; Gommers et al. 2013; Gundel et al. 2014). The root morphology is altered by the shoot-derived carbohydrate signals that have been suggested to play a role in the systemic control of the plant P-deficiency response. Exogenous supply of sucrose and increased light intensity both stimulate the formation of cluster roots in white lupin,

even when plants were under sufficient P supply (Zhou et al. 2008; Cheng et al. 2014).

Light influences the expression of genes associated with the low P responses by regulating the synthesis and transport of photosynthates (Hammond and White 2008). For example, the expression of *LaPEPC3* and *LaPT1*, which are induced by P starvation and associated with the exudation of citrate and P uptake, respectively, is upregulated when plants grow under high light intensity, regardless P supply (Cheng et al. 2014). Moreover, the expression of three P-responsive genes (*LaPT1*, *LaSAP1* and *LaMATE*) is downregulated in cluster roots of plants grown in darkness under a low P environment, indicating that the supply of photosynthates regulates the expression of these genes (Liu et al. 2005). Furthermore, the expression of *Atphl1;4*, which encodes a P transporter induced by P starvation, is reduced when plants are kept in the dark, but the presence of exogenous sucrose in the growth medium can sustain high expression of *Atphl1;4* (Karthikeyan et al. 2007). Light not only influences root morphology by regulating the synthesis and partitioning of photosynthates but also acts as a signal to directly regulate root growth (van Gelderen et al. 2018a). For example, far-red light detection in the shoot of *Arabidopsis* regulates lateral root growth via the HY5 transcription factor (Chen et al. 2016; van Gelderen et al. 2018b).

Maize, as an important food and feed, is widely cultivated around the world. Maize roots respond to P starvation by exhibiting extensive morphological alterations that contribute to the efficiency of P acquisition (Zhu et al. 2005, 2010; Zhang et al. 2012; Postma et al. 2014; Miguel et al. 2015). Similarly to many species of Poaceae, maize adapts to low soil P availability by altering root morphology, rather than root physiology (Lyu et al. 2016; Wen et al. 2017). However, whether and how the light intensity affects adaptive responses of root morphological traits to low soil P in maize has not been determined, especially in natural light conditions. Notably, most studies investigating the effects of light on root growth have been conducted in laboratories (e.g., Cheng et al. 2014; van Gelderen et al. 2018a), which might not reflect natural growth conditions. For example, a light intensity of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ is typical for the cultivation of plants in the laboratory, which is considerably lower than natural light intensities found under field conditions (light intensity usually reaches more than $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the field).

The main purpose of this study was to investigate how the light intensity influences maize root morphology, especially under low soil P conditions. In addition, we characterized the expression of low P tolerance transcript factor (*ZmPTF1*), which is associated with root growth by regulating carbon metabolism in leaves and roots (Li et al. 2011). The expressions of *ZmSPS1*, which encodes the key enzymes in the synthesis of sucrose in leaves, and *ZmSS2*, which is associated with sucrose decomposition in roots (Li et al. 2011), were also evaluated. Specifically, this study aimed to (1) quantify the dynamics of maize root growth in soil with variable P supply and under natural (NL) and low light (LL, 40% of natural light intensity) conditions; and (2) characterize how maize integrates the light intensity and P supply cues to improve root growth and P uptake in soil with P availabilities ranging from deficient to optimal to excess.

Materials and methods

The experiment was conducted in a naturally-lit rain-shed at the research farm of Sichuan Agricultural University, Chengdu (30°42' N, 103°51' E). The height of the rain-shed was 6 m, and the top of the shed was covered with thin and transparent plastic sheets to exclude rain. There was no wall around the rain-shed to maintain the similar air temperature inside and outside.

There were nine P application rates (0, 2.5, 5, 10, 25, 50, 75, 150 and 300 mg P kg⁻¹ soil, supplied as KH₂PO₄) and two light intensity treatments, natural light intensity (NL) and low light intensity (LL, 40% of natural light intensity). The crop growth was limited by light intensities lower than 50% of the natural under field conditions in the region of this study (Yang et al. 2014). Thus, a 40% natural light intensity was established as the low light intensity treatment by using shade cloth (Table S1). The shade cloth was supported by a stainless steel framework (3 × 3 × 3 m³). Under the shaded space, a time-controlled slow-speed fan was used to keep the air flow in the plant canopy. The periodic fanning was set as 30 min on and 30 min off during the day, and 30 min on and 60 min off during the night. The experiment was conducted from July 1st to August 5st, 2018. The daily light intensity and maximum and minimum air temperature during the plant growth period were obtained from the meteorological

station located nearby the experimental rain-shed, as shown in Fig. 1.

A sandy clay loam soil with low P availability was collected from a long-term fertilizer experiment in Renshou (30°06'N, 104°2'E). The soil was air-dried, sieved to 2-mm and thoroughly mixed. The soil properties were as follows: pH 6.72 (1:2.5, soil: water), Olsen-P 2.6 mg kg⁻¹, organic matter 8.6 g kg⁻¹, total N 0.31 g kg⁻¹, available K 84 mg kg⁻¹, and available N 80 mg kg⁻¹. Each pot (Φ 20 × 30 cm³) was filled with 5 kg of air-dried soil. To ensure the nutrient supply was adequate for plant growth, soil was fertilized with basal nutrients at the following rates (mg pot⁻¹): Ca(NO₃)₂·4H₂O 8435, CaCl₂ 630, MgSO₄·7H₂O 215, EDTA-FeNa 29, MnSO₄·4H₂O 33.5, ZnSO₄·7H₂O 50, CuSO₄·5H₂O 10.0, H₃BO₃ 3.35, and

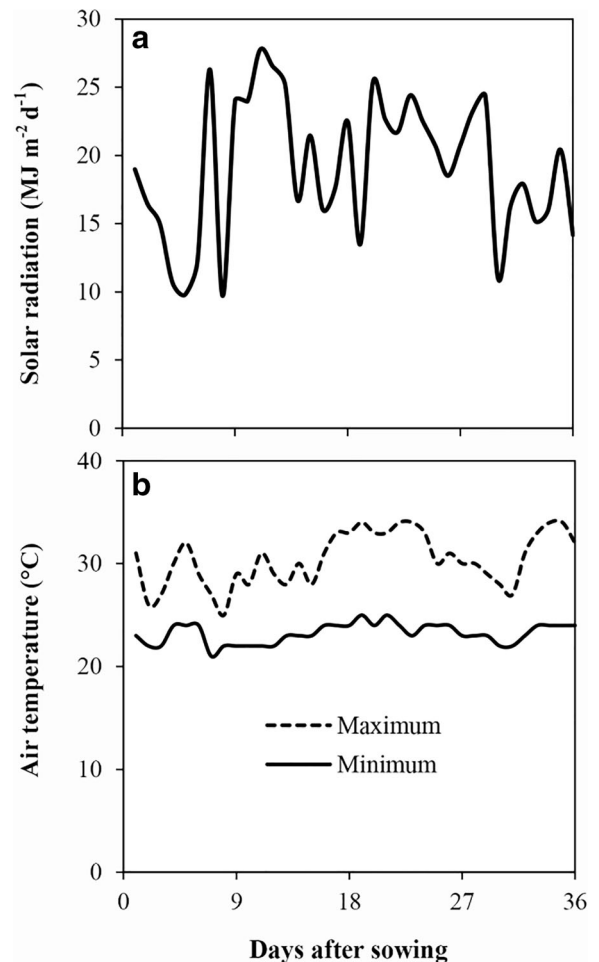


Fig. 1 Daily solar radiation (a) and minimum/maximum air temperature (b) during maize growth period, from July 1st to August 5st in 2018

(NH₄)₆Mo₇O₂₄·4H₂O 1.30. The P treatments were imposed by increasing the application of KH₂PO₄, and the equivalent K concentrations (1675 mg K pot⁻¹) were imposed using K₂SO₄. The fertilizers were manually mixed in the soil and homogenized 4 weeks before planting. After fertilization and homogenization, the soil Olsen-P concentrations were determined (Table 1).

Seeds of maize (*Zea mays* L.) cultivar CD418 (widely cultivated in the region) were surface-sterilized in 30% v/v H₂O₂ for 20 min and washed with deionized water before planting. Four uniformly germinated seeds were planted per pot, and the seedlings were thinned to two plants per pot at the 2-leaf stage. Three replicates were grown for each treatment, and pots were arranged in a split-plot design. The main plots consisted of NL and LL treatment, and the subplots were nine P application rates. All pots were watered daily until harvest.

Plant harvest and measurements of root morphology

After 36 d of growth (five leaf stage), the plants were harvested. The shoot and root subsamples were frozen in liquid nitrogen and stored at -80 °C until analysis of gene expression or sucrose concentration, and same subsamples were oven-dried at 80 °C for 3 d to measure dry weight and P concentration. Root subsamples were

washed with deionized water and scanned using an Epson Perfection V700 Photo scanner (Japan). Images were analyzed using WinRHIZO (WinRHIZO Pro2004, Canada) to measure root length and surface area. Fine roots were defined as roots with a diameter less than 0.2 mm (Jing et al. 2010).

Determination of net photosynthetic rate, P concentration, and sucrose concentration

Net photosynthetic rate (Pn) was measured on a youngest fully expanded leaf using a Li6400 photosynthesis system (Li-COR, Lincoln, NE, USA). Measurements were performed between 10:00 a.m. and 12:00 p.m. at the five-leaf stage.

The P concentrations were determined in leaves, stems and roots. The dry material was ground to pass through a 0.149-mm mesh sieve, a 0.3-g sample was digested with concentrated H₂SO₄ (5 mL) and H₂O₂ (30% v/v) (1 mL), and P was determined by the vanadomolybdate method (Page 1982).

The freeze-dried leaves and roots (FDU-2110, EYELA, Japan) were extracted in 80% v/v ethanol. Sucrose was measured directly in the extract, using resorcinol as the color reagent (Shi et al. 2016).

Table 1 Shoot and root dry weight of maize plants grown with different soil Olsen-P content under natural light intensity (NL) and low light intensity (LL, 40% of natural light intensity)

| P rate (mg P kg ⁻¹ soil) | Olsen-P (mg kg ⁻¹) | Shoot dry weight (g plant ⁻¹) | | Root dry weight (g plant ⁻¹) | |
|-------------------------------------|--------------------------------|---|---------------|--|---------------|
| | | NL | LL | NL | LL |
| 0 | 2.6 (0.10) f | 2.45 (0.30) f | 2.22 (0.26) f | 0.73 (0.16) d | 0.55 (0.03) e |
| 5 | 6.7 (0.08) e | 9.01 (0.15) d | 6.17 (0.66) e | 1.65 (0.16) b | 0.67 (0.04) d |
| 10 | 7.2 (0.09) e | 10.73 (0.23) c | 6.20 (0.52) e | 2.11 (0.10) a | 0.67 (0.05) d |
| 25 | 9.7 (0.11) e | 12.35 (0.40) b | 6.53 (0.86) e | 1.90 (0.19) a | 0.68 (0.11) d |
| 50 | 15.9 (0.23) d | 13.28 (0.48) a | 6.80 (1.06) e | 1.54 (0.04) b | 0.68 (0.11) d |
| 75 | 20.6 (0.23) d | 14.07 (0.71) a | 6.98 (0.63) e | 1.58 (0.05) b | 0.73 (0.08) d |
| 100 | 39.6 (0.56) c | 13.96 (0.56) a | 6.56 (0.17) e | 1.62 (0.13) b | 0.73 (0.09) d |
| 150 | 47.2 (0.66) b | 13.55 (0.33) a | 7.71 (0.91) e | 1.49 (0.38) c | 0.72 (0.06) d |
| 300 | 79.0 (1.50) a | 13.72 (0.78) a | 6.84 (0.29) e | 1.48 (0.05) c | 0.75 (0.02) d |
| ANOVA | | | | | |
| | P rate (P) | | <0.001 | | <0.000 |
| | Light intensity (L) | | <0.000 | | <0.000 |
| | P × L | | <0.021 | | <0.001 |

Plants were sampled at five-leaf stage after 36 d of growth. Values are means of three biological replicates (SE). Values for the NL and LL treatments at a given Olsen-P content followed by different lowercase letters are significantly different at $P \leq 0.05$

Quantitative real-time PCR analysis

Total RNA was isolated and treated with DNase I, and cDNA was synthesized to perform quantitative real time RT-PCR using the SYBR Green PCR Master Mix in the QuantStudio 6 Flex real-time PCR detection system (Thermo Fisher Scientific, USA) with appropriate primers. Relative expression of genes compared to the ACTIN was calculated using the $\Delta\Delta C_t$ method (Schmittgen and Livak 2008).

The primers used to quantify gene expression were as follows: *ZmPTF1*, 5'-ACACGGAAGAATCGGAAGACAC-3' and 5'-GGATATGGCGGAAGCAAGG-3'; *ZmSPS1*, 5'-ATGAGGGAGCGGCTGAGGAT-3' and 5'-GAGTGCCTGTGACCTTGATGCT-3'; *ZmSS2*, 5'-CTGCCTTACTCTGCCTGGTCT-3' and 5'-TTGGCCTTCTCGGTATGTGG-3'; *Zm38*, 5'-TGGATCAACTACCTCCGCC-3' and 5'-GCGATGAGCGACCACTTGTT-3'; *ZmACTIN*, 5'-ATGTGCTATCCAGGCTGTTCTT-3' and 5'-TGATCCTTCATAGATTGGAACCGT-3'.

Statistical analyses

Two-way analysis of variance was performed using the SPSS statistical software package (Version 19.0, SPSS Institute Inc., USA), and significant differences among P application rates were assessed using the LSD multiple range analysis test ($p \leq 0.05$) and using t tests to assess the significant differences between NL and LL treatments ($p \leq 0.05$).

The linear-plateau model was used to establish the relationship between shoot dry matter, root/shoot ratio and soil Olsen-P (Bai et al. 2013). Empirical polynomial (inverse third order) equations were used in Origin (Origin 16.0, USA) to analyze the relationship between root morphological traits (i.e., total root length, root surface area or proportion of fine roots) and soil Olsen-P (Deng et al. 2014).

Fertilizer P-use efficiency (PUE) was used to evaluate the P absorption efficiency of maize from P fertilizer applied to soil. PUE was calculated as follows:

$$\text{PUE (\%)} = \frac{U_f - U_0}{P_f} \times 100$$

where U_f is plant total P uptake by the P-treated crops, U_0 is plant total P uptake by the crops treated with zero

added P, and P_f is the amount of P fertilizer applied. The gap in PUE between the NL (NL_{PUE}) and LL treatments (LL_{PUE}) was calculated as $\Delta PUE = NL_{PUE} - LL_{PUE}$.

Results

Plant growth and biomass allocation

With the P application rate increasing from 0 to 300 mg P kg^{-1} soil, the soil Olsen-P increased from 2.6 to 79.0 mg kg^{-1} (Table 1). Compared to the zero P application, the P supply treatments increased shoot dry weight by up to 460% (NL) and 208% (LL), and increased root dry weight by up to 102% (NL) and 36.3% (LL), respectively (Table 1). Shoot and root dry weights were significantly higher in the NL compared with LL when plants were grown with P supply, but were not significantly affected by light intensity when plants were grown at 0-P addition (Table 1).

There was a strong positive correlation between shoot dry weight and soil P availability, with the soil Olsen-P increasing up to approximately 13.5 (NL) and 7.4 mg kg^{-1} (LL) and then leveling off (Fig. 2a). The ratio of root to shoot dry weight declined as soil Olsen-P increased to 10.8 (NL) and 7.3 mg kg^{-1} (LL) and then leveled off with a further increase in soil Olsen-P (Fig. 2b). Moreover, the root/shoot ratio was higher in the NL than LL treatments only when the soil Olsen-P was below 15.9 mg kg^{-1} (Table S2).

Root morphological traits

In the NL treatment, the total root length initially increased with increasing soil Olsen-P, peaking when the soil Olsen-P was approximately 7.2–15.9 mg kg^{-1} , and then gradually declined to a plateau (approximately 5100 cm plant^{-1}) (Fig. 3a). In the LL treatment, the total root length initially increased with increasing soil Olsen-P up to approximately 20 mg kg^{-1} and then leveled off (Fig. 3a). The effects of light intensity on root growth were more pronounced when plants were grown with low, rather than adequate P supply or zero-P supply. In the treatment with soil Olsen-P of 9.7 mg kg^{-1} , the total root length was 2-fold greater in NL than LL, but the total root length in NL and LL with no significant difference when soil Olsen-P was higher than 39.6 mg kg^{-1} (Table S2).

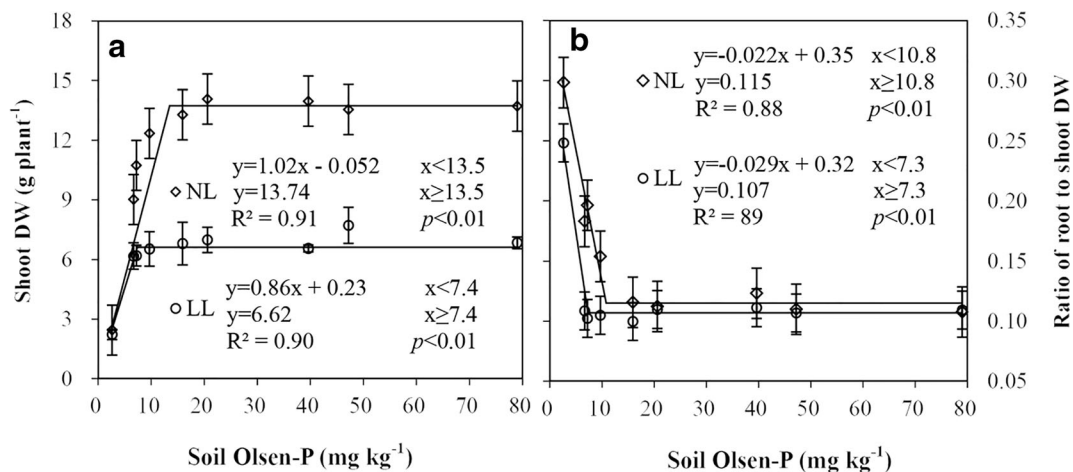


Fig. 2 Effects of P supply and light intensity on shoot dry weight (DW) (a) and the ratio of root to shoot DW (b). Each symbol represents the mean (\pm SE) of three replicates. NL = natural light intensity, LL = low light intensity (40% of natural light intensity)

The relationships between soil Olsen-P and root surface area or the fine root percentage were similar to total root length: in the NL treatment, the values of each of the root traits peaked in the Olsen-P range of 7.2–15.9 mg kg^{-1} followed by a decline to a plateau with a further increase in soil Olsen-P (Fig. 3b, c). In the LL treatment, root surface area initially increased with increasing soil Olsen-P up to the critical value and then leveled off (Fig. 3c). The effect of light intensity was obvious when plants were grown with a low (6.7 to 15.9 mg kg^{-1}), rather than with an adequate P supply. However, the fine root percentage decreased with increasing soil Olsen-P under LL (Fig. 3b). Additionally, in the treatments with soil Olsen-P ranging from 6.7 to 15.9 mg kg^{-1} , the fine root percentage was higher in NL than LL (Table S2).

Shoot P status, plant P uptake and fertilizer P use efficiency

Leaf P concentration increased with increasing soil Olsen-P up to 15.9 mg kg^{-1} and then leveled off regardless of light intensity (Fig. 4a). With increases in light intensity from LL to NL, leaf P concentration decreased in the treatments with relatively low soil Olsen-P, but not in the treatments with zero-P addition or soil Olsen-P higher than 20.6 mg kg^{-1} (Fig. 4a). Root P concentrations in the treatments were lower under NL than LL regardless of P supply (Fig. 4b). The *ZmPTF1* (associated with root growth) was highly expressed under P deficiency, and the increased light intensity stimulated the expression further (Fig. 4d). In addition, the

expression of *Zm38* (a low P response transcription factor) shared the same trend as *ZmPTF1* (Fig. 4e). Indeed, P acquisition significantly increased from LL to NL when P had been supplied (Fig. 4c, f).

The fertilizer P use efficiency (PUE) decreased with increasing P fertilizer, regardless of light intensity. However, in the treatments with soil Olsen-P below 39.6 mg kg^{-1} , the PUE was significantly higher in NL than in LL (Fig. 5a). The PUE gap between NL and LL reached a maximum (22.5%) when soil Olsen-P was 7.2 mg kg^{-1} , but declined with increasing soil Olsen-P (Fig. 5b).

Photosynthetic efficiency and carbohydrate accumulation in leaves and roots

In the NL treatment, net photosynthesis (Pn) increased with increasing soil Olsen-P up to 39.6 mg kg^{-1} , and then leveled off (Fig. 6a). However, the Pn showed no response to P supply in the LL treatment (Fig. 6a). Net photosynthesis increased significantly from LL to NL regardless of P supply (Fig. 6a).

The leaf sucrose concentration generally followed similar trends as Pn under the variable soil Olsen-P and light treatments (Fig. 6b): Leaf sucrose concentration was significantly higher in the treatments under NL than LL. Moreover, leaf sucrose concentration was also increased with increasing P supply, especially under NL (Fig. 6b). The gene *ZmSPS1* encoding the key enzymes participating in the synthesis of sucrose in leaves was expressed more strongly under NL than LL, and the expression was also stimulated with low-P supply (Fig. 6c).

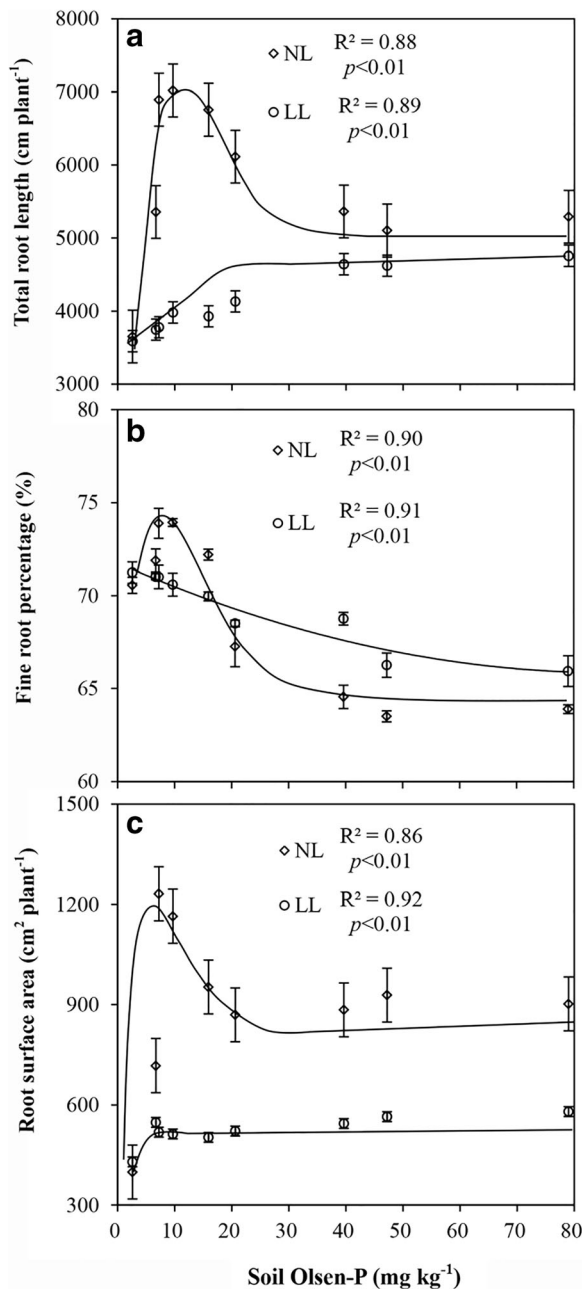


Fig. 3 Maize root morphological traits in response to increasing soil Olsen-P and light intensity: (a) total root length, (b) fine root (diameter ≤ 0.2 mm) percentage over total root length, (c) total root surface area. Each symbol represents the mean (\pm SE) of three replicates. NL = natural light intensity, LL = low light intensity (40% of natural light intensity)

The root sucrose concentration increased from LL to NL, regardless of P supply (Fig. 6c). Moreover, this concentration was higher in the treatments with low than sufficient P supply. The *ZmSS2* (involved in sucrose

decomposition in root) was highly expressed under low P conditions, and decreasing light intensity stimulated the expression of *ZmSS2* further (Fig. 6f). Additionally, the ratio of root to shoot sucrose was higher in NL than LL with soil Olsen-P values ranging from 2.6 to 15.9 mg kg⁻¹ (Fig. 6d).

Correlations between total root length and P concentration in leaves, and sucrose concentration in roots

The root sucrose concentration was inversely related to leaf P concentration: the root sucrose concentration decreased with increasing leaf P concentration regardless of light conditions (Fig. 7a). The total root length was positively related to the leaf P concentration and sucrose concentration in roots in the NL treatment, and the relationships between root length and leaf P or root sucrose were approximated to a parabola (Fig. 7b, c). In the LL treatment, total root length was negatively related to the leaf P concentration and sucrose concentration in roots (Fig. 7b, c).

Discussion

Maize growth in response to variable soil P availability and light intensity

Maize growth first increased with an increase in soil Olsen-P and then leveled off when soil Olsen-P surpassed the critical value. For example, the critical soil Olsen-P values ranged from 13 to 15 mg kg⁻¹ for maize and 11 to 15 mg kg⁻¹ for wheat in long-term P application experiments in China (Tang et al. 2009). In Europe, the critical soil Olsen-P values ranged from 7 to 18 mg kg⁻¹ (Poulton et al. 2013; Colomb et al. 2007; Bollons and Barraclough 1999). The critical soil Olsen-P value for maize (14.6 mg kg⁻¹) grown in northwestern China with high solar radiation was higher than that in the same region (11.1 mg kg⁻¹) of this study with low solar radiation (Bai et al. 2013). The data reported here indicated the critical soil Olsen-P value for shoot dry weight production was higher under NL (13.5 mg kg⁻¹) than LL (7.4 mg kg⁻¹) (Fig. 2a). This result may indicate the promotion of high light intensity in root growth and P acquisition (Hammond and White 2008; Gao et al. 2017).

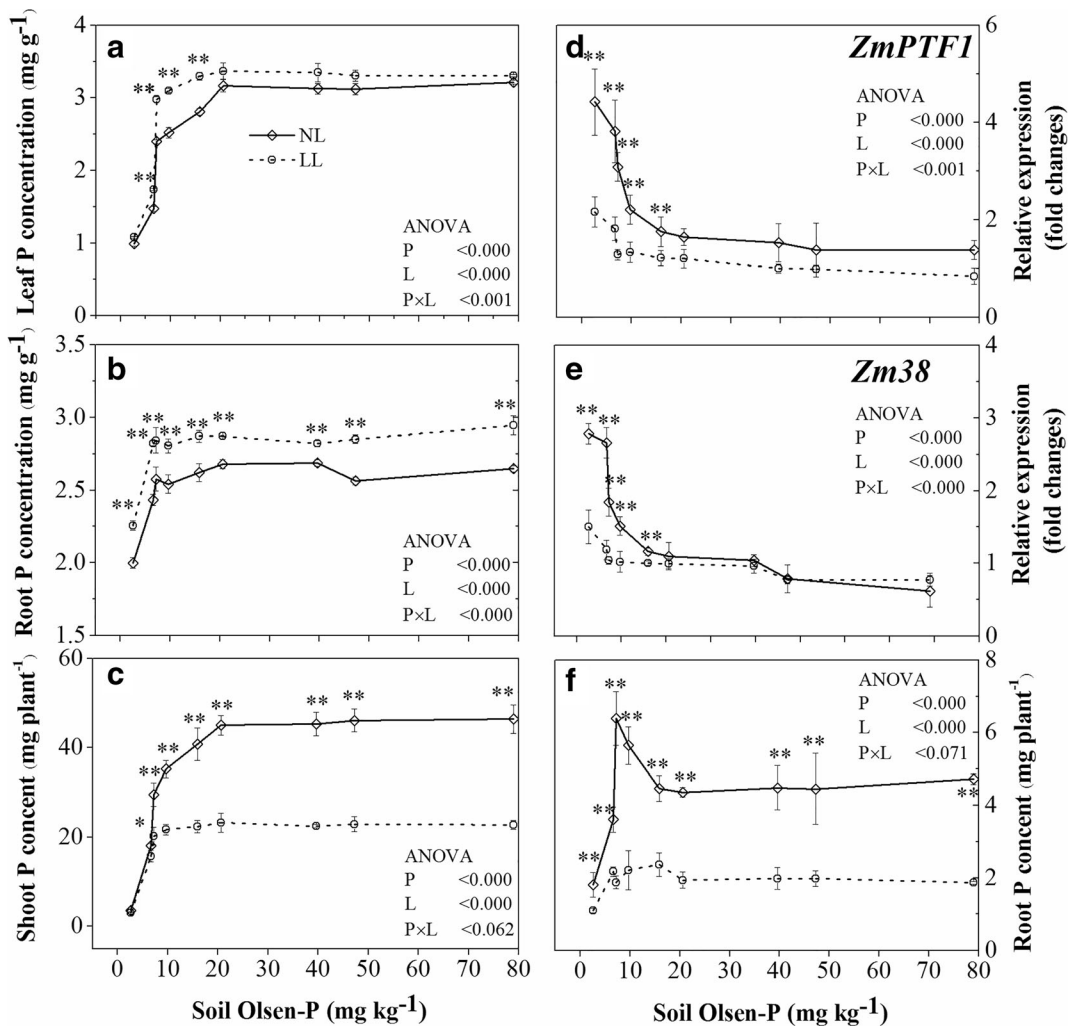


Fig. 4 Effects of P supply and light intensity on maize P status (a: leaf P concentration, b: root P concentration, c: shoot P content, f: root P content) and the expression of the low-P tolerance transcription factor *ZmPTF1* (d) and low-P response gene *Zm38* (e). Each symbol represents the mean (\pm SE) of three replicates. NL = natural light intensity, LL = low light intensity (40% of natural light intensity). For *ZmPTF1* expression, data are expressed as relative

values based on the expression of *ZmPTF1* in roots grown with soil Olsen-P 39.6 mg kg⁻¹ under LL referenced as 1.0. For *Zm38* expression, data are expressed as relative values based on the expression of *Zm38* in root grown with soil Olsen-P 39.6 mg kg⁻¹ under LL referenced as 1.0. *and** indicated significant difference between the NL and LL treatments at a given soil Olsen-P content (*t*-test at $p \leq 0.05$ and $p \leq 0.01$, respectively)

Many previous studies have reported that both P-deficiency and high light intensity increase the ratio of root to shoot dry weight, which was associated with increased carbohydrate concentration in roots (Cruz 1997; Hébert et al. 2001; Ciereszko and Barbachowska 2000; Hammond and White 2008, 2011). Similarly, in the study presented here P-deficiency increased the ratio of root to shoot dry weight and root sucrose concentration; moreover an increase in light intensity from LL to NL enhanced the root sucrose concentration further (Table 1, Figs. 2b and 6c).

However, the light intensity had no significant effects on the root to shoot ratio when the soil Olsen-P surpassed the critical value (Fig. 2b). The soil Olsen-P for maize growth in the present study ranged from 2.6 to 79.0 mg kg⁻¹, covering deficiency, optimum and excess (Table 1). As expected, the plant growth showed a positive response to increased light intensity and P supply (Table 1, Figs. 2b and 6d), suggesting that the experimental conditions were suitable for estimating the root morphological responses to the variable soil P availability and light intensity.

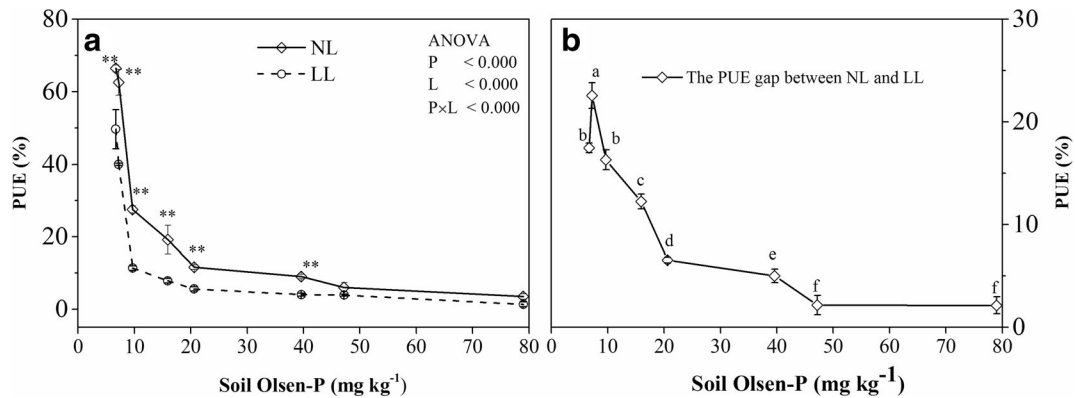


Fig. 5 Effects of P supply and light intensity on maize fertilizer P use efficiency (**a**: PUE, **b**: the PUE gap between the treatments NL and LL). Each symbol represents the mean (\pm SE) of three replicates. NL = natural light intensity, LL = low light intensity (40% of

natural light intensity). ** indicated significant difference between the NL and LL treatments at a given soil Olsen-P content (*t*-test at $p \leq 0.01$). Letters are significantly different among P application rates at $p \leq 0.05$

Root morphological response to leaf P concentration

In many species of Poaceae (such as maize, wheat, and rice), root morphological plasticity is the major response to low P stress and plays an important role in P uptake (Pearse et al. 2006, 2007; Nuruzzaman et al. 2006; Lyu et al. 2016; Wen et al. 2017). It is generally accepted that the root morphological plasticity response to P-deficiency was mainly triggered by internal P status (leaf P status) rather than external P concentration (Li et al. 2008; Lambers et al. 2011; Pang et al. 2009). For example, the leaf P status regulated the formation of cluster roots in white lupin grown with a divided root system, in which one root half was supplied with P and the other half was not (Shane et al. 2003). Moreover, leaf P status also regulated the root morphological (root/shoot ratio, fine root percentage, and specific root length) traits of maize in responses to low P stress (Wen et al. 2017). In the present study, the expressions of *ZmPTF1* (associated with root growth) (Fig. 4d) and *Zm38* (low P response gene) (Fig. 4e) was corresponded well with the P concentration in leaves, not in root (Fig. 4a, b), suggesting that root growth might be affected by a leaf P status.

In the present study, a wide range of root morphological changes were observed in response to altered light intensity under variable P environments (Table S2, Fig. 3). Leaf P concentration was the lowest in the treatments with soil Olsen-P of 2.6 mg kg⁻¹, regardless of light intensity (Fig. 4a), and the total root length and root surface area were severely inhibited, with no significant difference between NL and LL

(Table S2). These findings suggested leaf growth and photosynthesis were impaired at extremely low P (Mollier and Pellerin 1999; Plénet et al. 2000), which subsequently inhibited root growth and function. Maize had higher total root length (Fig. 3a), total root surface (Fig. 3c) and fine root percentage (Fig. 3b) when grown at low Olsen-P (6.7 to 15.9 mg kg⁻¹) under NL than LL. These finding might have been due to an increase in light intensity from LL to NL increasing both Pn (Fig. 6a) and carbon fixation (Fig. 6b), followed by a growth-induced P-starvation signal (Fig. 4a) enhancing root morphological responses to low P stress. These results were consistent with findings in lupin, soybean, and maize, whereby plants with more light capture increased the photosynthesis and shoot growth, thus (1) increasing shoot P demand that might have exceeded the capacity of roots to supply P to leaves, (2) causing growth-induced P-starvation in the shoot, and (3) producing a systemic signal to induce root morphological responses to low P stress (Cheng et al. 2014; Zhou et al. 2019). Fine roots in maize are critical for nutrient uptake (Zhang et al. 2012; Li et al. 2016b) and are regulated by the leaf P status (Wen et al. 2017). High light intensity increases the percentage of fine roots may be an efficient strategy for maize to adapt to P-deficiency (Fig. 3b), with increased total root length and surface area to improve P uptake capacity achieved at a minimal carbon cost (Zobel et al. 2007; Pang et al. 2009; Lambers et al. 2006; Lynch 2015). The low-P tolerance transcription factor *ZmPTF1*, which promotes root growth, was expressed in roots at a higher level under NL than LL, and corresponded well with the P concentration in leaf

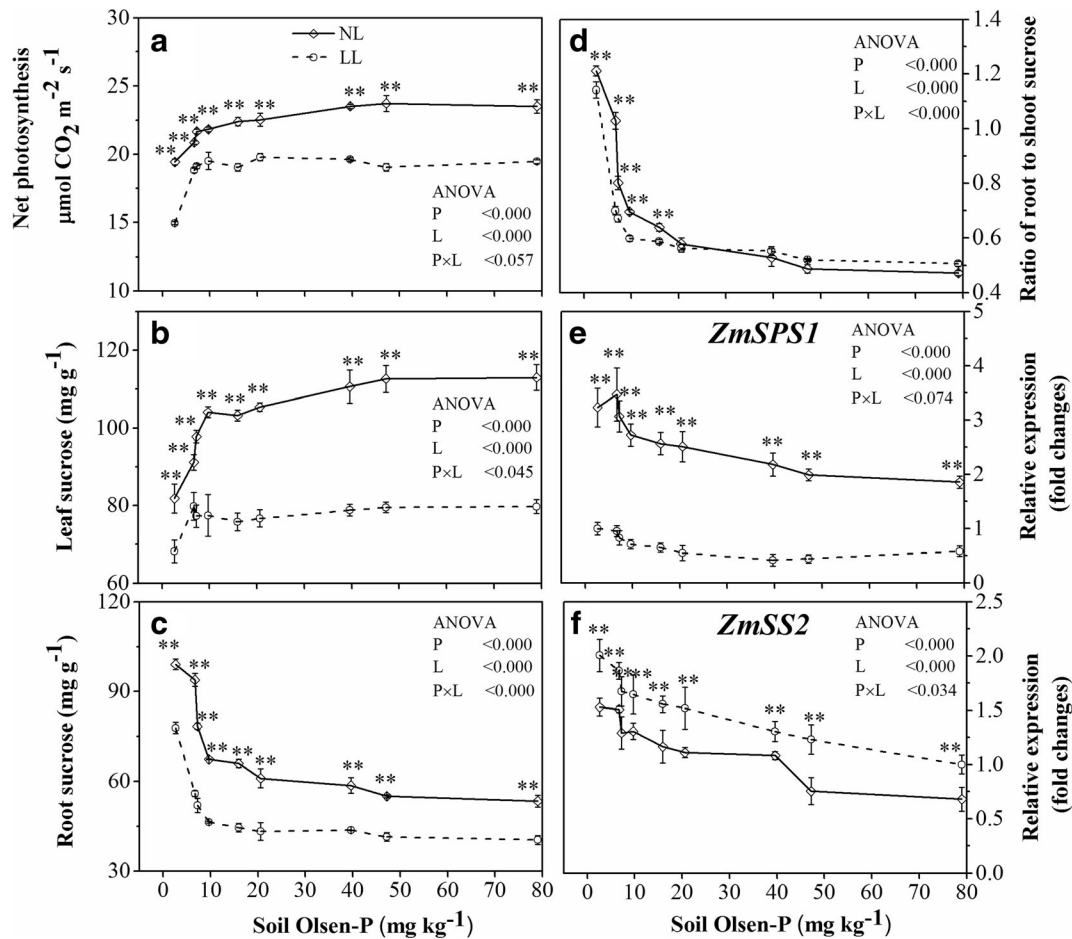


Fig. 6 Effects of P supply and light intensity on maize net photosynthetic (P_n) rate (**a**), sucrose status (**b**: leaf sucrose concentration, **c**: root sucrose concentration), ratio of root to shoot sucrose (**d**), and the expression of the key enzymes in the sucrose synthesis (**e**: *ZmSPS1*, **f**: *ZmSS2*). Each symbol represents the mean (±SE) of three replicates. NL = natural light intensity, LL = low light intensity (40% of natural light intensity). For *ZmSPS1* expression, data are expressed as relative values based on the expression of

ZmSPS1 in leaves of plants grown with soil Olsen-P 2.6 mg kg⁻¹ under LL referenced as 1.0. For *ZmSS2* expression, data are expressed as relative values based on the expression of *ZmSS2* in roots of plants grown with soil Olsen-P 79.0 mg kg⁻¹ under LL referenced as 1.0. ** indicated significant difference between the NL and LL treatments at a given soil Olsen-P content (*t*-test at *p* ≤ 0.01)

(Fig. 4a, d), providing additional evidence that relatively low P concentrations in leaves under NL than LL (Fig. 4a) enhanced root growth.

With soil Olsen-P above 20.6 mg kg⁻¹, the root traits (total root length, total root surface, and fine root percentage) were relatively low and stable (Table S2, Fig. 3). Moreover, leaf P concentrations were relatively high, and expressions of both *ZmPTF1* and *Zm38* were relatively low; for all these variables there was no significant difference between NL and LL (Fig. 4a, d, e), suggesting that the effects of light intensity on root growth decreased at sufficient and excess P (with soil

P availability not a limiting factor) compared to low P supply (see also Chiou and Lin 2011; Wen et al. 2017).

The quadratic models fit the relationship between total root length and leaf P concentration well in the NL treatment, with the low leaf P concentration (up to 2.3 mg g⁻¹), inducing root growth (Fig. 7b). However, in the LL treatment, the total root length was not positively related to leaf P concentration (Fig. 7b), which indicated that P was not the main limiting factor under low light intensity (cf. Wissuwa et al. 2005; Cheng et al. 2014). A similar experiment (Wen et al. 2017) conducted with a wide range of soil showed that when the maize

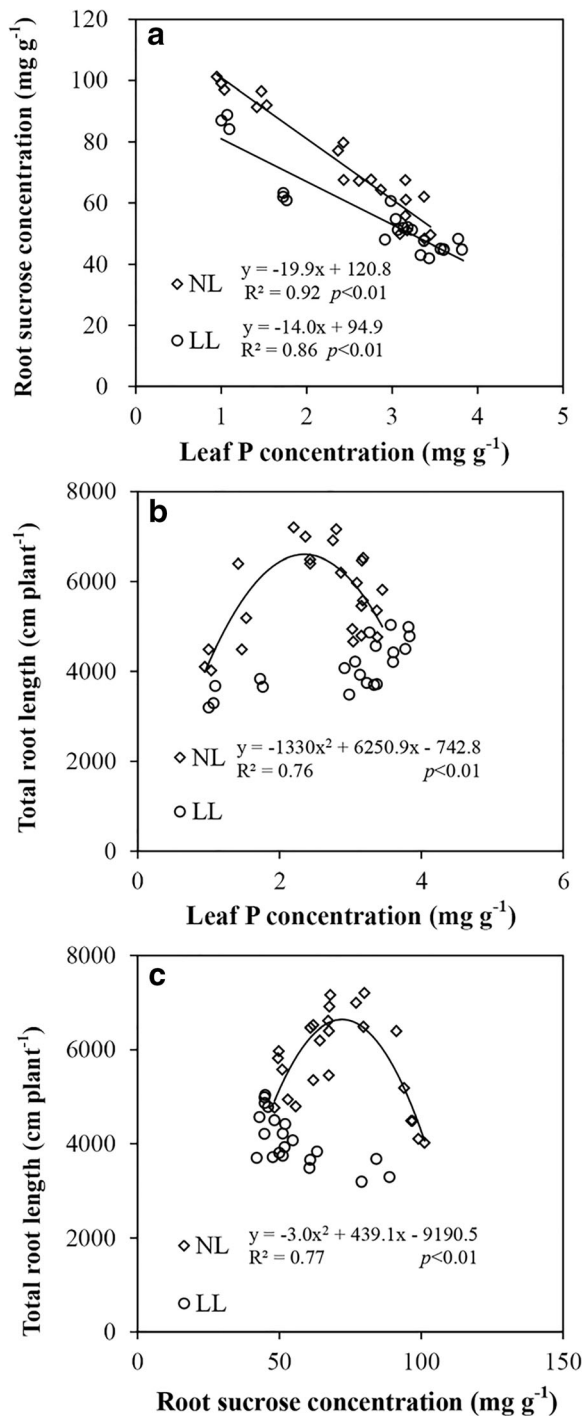


Fig. 7 Correlations between leaf P concentration and root sucrose concentration (a). Correlations between total root length and leaf P concentration (b) or root sucrose concentration (c). Data points represent individual replicates. NL = natural light intensity, LL = low light intensity (40% of natural light intensity)

leaf P concentration ranged from 1 to 2 mg g^{-1} , the total root length, specific root length, and fine root percentage increased with increasing leaf P; in contrast, the root morphological traits were relatively low and stable when the leaf P concentration was higher than 2.7 mg g^{-1} . The critical leaf P values between the two experiments were different, as the various results might be due to different maize genotypes and growth conditions (i.e., temperature and light intensity) or soil properties. However, these results indicated that light intensity stimulated the root morphological traits response to P starvation by influencing leaf P status.

Root morphological responses to carbohydrate metabolism in leaves and roots

Plants with insufficient P showed reduced shoot growth rates and translocated carbohydrate in excess of their shoot growth capacity to roots, which resulted in relatively high carbohydrate concentration in roots (Rychter and Randall 1994; Hermans et al. 2006; Hammond and White 2008, 2011; Niu et al. 2012). Similarly, increasing light intensity also increased translocation of carbohydrates to roots (Cruz 1997; Hébert et al. 2001; Lemoine et al. 2013; Zhou et al. 2019). Stem girdling has been used to explore the importance of photosynthates in P-deficiency signaling. For example, in white lupin stem girdling to block phloem translocation to roots resulted in a significant reduction in the expression of the low P response genes *LaPT1* and *LaSAP1* (Liu et al. 2005). Similar results were also obtained in common bean (Liu et al. 2010). Taken together, the results of these studies suggest that carbohydrates (such as sucrose) serve as both a low P signal and a carbon-substrate for roots growth to increase the P foraging capacity (i.e. low P adaptations) (Hermans et al. 2006; Müller et al. 2007; Hammond and White 2008; Liu et al. 2005; Zhou et al. 2008). The findings of the study presented here were consistent with the observations that both P-deficiency and increasing light intensity increased translocation of sucrose to roots (Fig. 6d) and root sucrose concentration (Fig. 6c). However, how maize integrates sucrose- and P-based regulation of root growth with a wide range of soil P availability requires further investigation.

Increased light intensity from LL to NL increased the net photosynthetic rate of maize with soil Olsen-P covering deficiency, optimum and excess. However, net photosynthesis was impaired when maize was grown with extremely low soil P availability regardless of light

intensity (Fig. 6a), which was consistent with the results obtained with other species (Rao et al. 1990; Wissuwa et al. 2005; Cheng et al. 2014). The root sucrose concentration was the highest in the treatment with soil Olsen-P of 2.6 mg kg⁻¹, regardless of light intensity (Fig. 6c), but the root growth was severely inhibited (Table S2) due to severe root P-starvation (Fig. 4b). Similarly, in rice and white lupin under extreme P-starvation, the carbohydrates supply was not limiting root growth (Wissuwa et al. 2005; Cheng et al. 2014).

When soil Olsen-P increased from 6.7 to 15.9 mg kg⁻¹, more photosynthates were allocated to roots as sucrose under NL than LL (Fig. 6c, d), which was associated with greater total root length and fine root percentage (Fig. 3a, b). Enhanced translocation of carbohydrates to roots and enhanced total root length were the universal responses to P deficiency in maize (Mollier and Pellerin 1999; Zhang et al. 2012; Deng et al. 2014) because P-deficient plants invested more carbon to root growth to improve the P acquisition capacity (Fernandez and Rubio 2015; Hammond and White 2008; Ruan 2014).

In excess P supply, natural light did not enhance the allocation of sucrose to the roots between the NL and LL treatments (Fig. 6d). Furthermore, there was also no significant difference in the total root length between the two light treatments (Table S2). One possible explanation might be that P-sufficient plants lacked a P-starvation signal associated with increased carbon investment to root growth and increased P acquisition capacity (Shiple and Meziane 2002; Poorter et al. 2012). Like the expression of *ZmPTF1*, which is associated with root growth by allocating carbon to root, was downregulated and showed no significant difference between NL and LL in the treatments with sufficient P supply (Fig. 4d). The quadratic model fit the relationship between total root length and root sucrose concentration well in NL (Fig. 7c), indicating that light intensity enhanced the root morphological adaptations response to P starvation by regulating root sucrose concentration.

Direct root morphological responses to light conditions

Stimulation of root growth by increased light intensity might not be controlled exclusively by increased allocation of sucrose to roots; instead, other systemic signals

(such as phytohormone) could also contribute to root growth. For example, auxin was found to stimulate root growth in maize, particular in low P conditions (Martínez-de la Cruz et al. 2015; Li et al. 2018; Zhang et al. 2019). High light intensity enhanced sensitivity of cluster root formation to auxin by downregulating the expression of an auxin-response repressor gene (Cheng et al. 2014), whereas sucrose increased the sensitivity of lateral root development to auxin in P-deficient *Arabidopsis* (Jain et al. 2007). In the present study, the expression of the auxin response factor (ARF), which activates the auxin-induced gene expression response, was found to be upregulated under NL, especially under low P conditions (data not shown). In addition, light could also enhance the biosynthesis of indole-3-acetic acid (Bhalerao et al. 2002): specifically, light increases flavonol biosynthesis, which increases root auxin levels (Buer and Muday 2004; Silva-Navas et al. 2016). Except for the sensitivity and formation, light can also affect the transportation of auxin in the root by controlling the removal of PIN proteins from the plasma membrane via the process of vacuolar degradation (Korbei and Luschnig 2013). Further work is needed to elucidate a role of auxins in the light- and P-availability-dependent regulation of root growth.

Conclusion

Our results demonstrated that an increase in light intensity enhanced total root length, root surface area, and fine root percentage, underpinning increased P acquisition and P use efficiency, especially at low soil P availability (soil Olsen-P from 6.7 to 15.9 mg kg⁻¹). These effects diminished in soil with either severely low P (soil Olsen-P 2.6 mg kg⁻¹) or excess P (soil Olsen-P above 20.6 mg kg⁻¹). Maize may integrate the environmental cues (P supply and light intensity) to regulate leaf P status and root sucrose concentration to determine plant growth. It is possible that photosynthesis and the leaf P status coordinate the morphological responses of roots by controlling the transfer of carbohydrates to roots.

Acknowledgments This work was supported by the National Key Research and Development Program of China (2016YFD0300109-3) and National Natural Science Foundation of China (31771728 and 31671626).

References

- Bai ZH, Li HG, Yang XY, Zhou BK, Shi XJ, Wang BR, Li DC, Shen JB, Chen Q, Qin W, Oenema O, Zhang FS (2013) The critical soil P levels for crop yield, soil fertility and environmental safety in different soil types. *Plant Soil* 372:27–37
- Bhalerao RP, Eklöf J, Ljung K, Marchant A, Bennett M, Sandberg G (2002) Shoot-derived auxin is essential for early lateral root emergence in *Arabidopsis* seedlings. *The Plant J* 29:325–332
- Bollons HM, Barraclough PB (1999) Assessing the phosphorus status of winter wheat crops: inorganic orthophosphate in whole shoots. *J Agric Sci* 133:285–295
- Buer CS, Muday GK (2004) The *transparent testa4* mutation prevents flavonoid synthesis and alters auxin transport and the response of *Arabidopsis* roots to gravity and light. *Plant Cell* 16:1191–1205
- Chen X, Yao Q, Gao X, Jiang C, Harberd NP, Fu X (2016) Shoot-to-root mobile transcription factor HY5 coordinates plant carbon and nitrogen acquisition. *Curr Biol* 26:640–646
- Cheng L, Tang X, Vance CP, White PJ, Zhang F, Shen J (2014) Interactions between light intensity and phosphorus nutrition affect the phosphate-mining capacity of white lupin (*Lupinus albus* L.). *J Exp Bot* 65:2995–3003
- Chiou TJ, Lin SI (2011) Signaling network in sensing phosphate availability in plants. *Ann Rev Plant Biol* 62:185–206
- Ciereszko I, Barbachowska A (2000) Sucrose metabolism in leaves and roots of bean (*Phaseolus vulgaris* L.) during phosphate deficiency. *J Plant Physiol* 156:640–644
- Colomb B, Debaeke P, Jouany C, Nolot JM (2007) Phosphorus management in low input stockless cropping systems: crop and soil responses to contrasting P regimes in a 36-year experiment in southern France. *Eur J Agron* 26:154–165
- Cruz P (1997) Effect of shade on the carbon and nitrogen allocation in a perennial tropical grass, *Dichanthium aristatum*. *J Exp Bot* 48:15–23
- Deng Y, Chen K, Teng W, Zhan A, Tong Y, Feng G, Cui Z, Zhang F, Chen X (2014) Is the inherent potential of maize roots efficient for soil phosphorus acquisition? *PLoS One* 9:e90287. <https://doi.org/10.1371/journal.pone.0090287>
- Fernandez MC, Rubio G (2015) Root morphological traits related to phosphorus-uptake efficiency of soybean, sunflower, and maize. *J Plant Nutr Soil Sci* 178:807–815
- Gao J, Shi J, Dong S, Liu P, Zhao B, Zhang J (2017) Grain yield and root characteristics of summer maize (*Zea mays* L.) under shade stress conditions. *J Agron Crop Sci* 203:562–573
- van Gelderen K, Kang C, Pierik R (2018a) Light signaling, root development, and plasticity. *Plant Physiol* 176:1049–1060
- van Gelderen K, Kang C, Paalman R (2018b) Far-red light detection in the shoot regulates lateral root development through the *HY5* transcription factor. *Plant cell tpc-00771*. <https://doi.org/10.1105/tpc.17.00771>
- Gommers CMM, Visser EJW, St Onge KR, Voeselek LACJ, Pierik R (2013) Shade tolerance: when growing tall is not an option. *Trends Plant Sci* 18:65–71
- Gundel PE, Plerik R, Mommer L, Ballaré CL (2014) Competing neighbors: light perception and root function. *Oecologia* 176:1–10
- Hammond JP, White PJ (2008) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. *J Exp Bot* 59:93–109
- Hammond JP, White PJ (2011) Sugar signaling in root responses to low phosphorus availability. *Plant Physiol* 156:1033–1040
- Hébert Y, Guingo E, Loudet O (2001) The response of root/shoot partitioning and root morphology to light reduction in maize genotypes. *Crop Sci* 41:363–371
- Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? *Trends Plant Sci* 11:610–617
- Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil* 237:173–195
- Jain A, Poling MD, Karthikeyan AS, Blakeslee JJ, Peer WA, Titapiwatanakun B, Murphy AS, Raghothama KG (2007) Differential effects of sucrose and auxin on localized phosphate deficiency-induced modulation of different traits of root system architecture in *Arabidopsis*. *Plant Physiol* 144:232–247
- Jing J, Rui Y, Zhang F, Rengel Z, Shen J (2010) Localized application of phosphorus and ammonium improves growth of maize seeding by stimulating root proliferation and rhizosphere acidification. *Field Crop Res* 119:355–364
- Johnston AE, Poulton PR, Fixen PE, Curtin D (2014) Phosphorus: its efficient use in agriculture. *Adv Agron* 123:177–228
- Karthikeyan AS, Varadarajan DK, Jain A, Held MA, Carpita NC, Raghothama KG (2007) Phosphate starvation responses are mediated by sugar signaling in *Arabidopsis*. *Planta* 225:907–918
- Korbei B, Luschnig C (2013) Plasma membrane protein ubiquitylation and degradation as determinants of positional growth in plants. *J Integr Plant Biol* 55:809–823
- Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Ann Bot* 98:693–713
- Lambers H, Finnegan PM, Laliberte E, Pearse SJ, Ryan MH, Shane MW, Veneklaas EJ (2011) Update on phosphorus nutrition in Proteaceae. Phosphorus nutrition of proteaceae in severely phosphorus-impooverished soils: are there lessons to be learned for future crops? *Plant Physiol* 156:1058–1066
- Lemoine R, La Camera S, Atanassova R, Dédaldéchamp F, Allario T, Pourtau N, Bonnemain J, Laloï M, Coutos-Thévenot P, Maurousset L, Faucher M, Girousse C, Lemonnier P, Parrilla J, Durand M (2013) Source-to-sink transport of sugar and regulation by environmental factors. *Front Plant Sci* 4. <https://doi.org/10.3389/fpls.2013.00272>
- Li L, Li SM, Sun JH, Zhou LL, Bao XG, Zhang HG, Zhang FS (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *P Natl Acad Sci USA* 104:11192–11196
- Li H, Shen J, Zhang F, Tang C, Lambers H (2008) Is there a critical level of shoot phosphorus concentration for cluster-root formation in *Lupinus albus*? *Concentr Plant Biol* 35:328–336
- Li ZX, Gao Q, Liu YZ, He CM, Zhang XR, Zhang JR (2011) Overexpression of transcription factor *ZmPTF1* improves low phosphate tolerance of maize by regulating carbon metabolism and root growth. *Planta* 233:1129–1143
- Li L, Tilman D, Lambers H, Zhang FS (2014) Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytol* 203:63–69

- Li XX, Zeng RS, Liao H (2016a) Improving crop nutrient efficiency through root architecture modifications. *J Inter Plant Biol* 58:193–202
- Li Y, Niu S, Yu G (2016b) Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. *Glob Chang Biol* 22:934–943
- Li ZX, Zhang XR, Zhao YJ, Li YJ, Zhang GF, Peng ZH, Zhang JR (2018) Enhancing auxin accumulation in maize root tips improves root growth and dwarfs plant height. *Plant Biotechnol J* 16:86–99
- Liu J, Samac DA, Bucciarelli B, Allan DL, Vance CP (2005) Signaling of phosphorus deficiency-induced gene expression in white lupin requires sugar and phloem transport. *Plant J* 41:257–268
- Liu JQ, Allan DL, Vance CP (2010) Systemic signaling and local sensing of phosphate in common bean: cross-talk between photosynthate and microRNA399. *Mol Plant* 3:428–437
- Lynch JP (2015) Root phenes that reduce the metabolic costs of soil exploration: opportunities for 21st century agriculture. *Plant Cell Environ* 38:1775–1784
- Lyu Y, Tang H, Li H, Zhang F, Rengel Z, Whalley WR, Shen J (2016) Major crop species show differential balance between root morphological and physiological responses to variable phosphorus supply. *Front Plant Sci* 7. <https://doi.org/10.3389/fpls.2016.01939>
- Martínez-de la Cruz E, García-Ramírez E, Vázquez-Ramos JM, Reyes de la Cruz H, López-Bucio L (2015) Auxins differentially regulate root system architecture and cell cycle protein levels in maize seedlings. *J Plant Physiol* 176:147–156
- Mehra P, Pandey BK, Giri J (2016) Improvement in phosphate acquisition and utilization by a secretory purple acid phosphatase (*OsPAP21b*) in rice. *Plant Biotechnol J* 15:1054–1067
- Miguel MA, Postma JA, Lynch JP (2015) Phene synergism between root hair length and basal root growth angle for phosphorus acquisition. *Plant Physiol* 167:1430–1439
- Mollier A, Pellerin S (1999) Maize root system growth and development as influenced by phosphorus deficiency. *J Exp Bot* 50:487–497
- Müller R, Morant M, Jarmer H, Nilsson L, Nielsen TH (2007) Genome-wide analysis of the Arabidopsis leaf transcriptome reveals interaction of phosphate and sugar metabolism. *Plant Physiol* 143:156–171
- Niu YF, Chai RS, Jin GL, Wang H, Tang CX, Zhang YS (2012) Responses of root architecture development to low phosphorus availability: a review. *Ann Bot* 112:391–408
- Nuruzzaman M, Lambers H, Bolland M, Veneklaas EJ (2006) Distribution of carboxylates and acid phosphatase and depletion of different phosphorus fractions in the rhizosphere of a cereal and three grain legumes. *Plant Soil* 281:109–120
- Page AL (1982) Methods of soil analysis (part 2), 2nd edn. American Society of Agronomy, Madison
- Pang J, Ryan MH, Tibbett M, Cawthray GR, Siddique KHM, Bolland MDA, Denton MD, Lambers H (2009) Variation in morphological and physiological parameters in herbaceous perennial legumes in response to phosphorus supply. *Plant Soil* 331:241–255
- Pearse SJ, Veneklaas EJ, Cawthray G, Bolland MD, Lambers H (2006) *Triticum aestivum* shows a greater biomass response to a supply of aluminium phosphate than *Lupinus albus*, despite releasing fewer carboxylates into the rhizosphere. *New Phytol* 169:515–524
- Pearse SJ, Veneklaas EJ, Cawthray G, Bolland MD, Lambers H (2007) Carboxylate composition of root exudates does not relate consistently to a crop species' ability to use phosphorus from aluminium, iron or calcium phosphate sources. *New Phytol* 173:181–190
- Plénet D, Etchebest S, Mollier A, Pellerin S (2000) Growth analysis of maize field crops under phosphorus deficiency. *Plant Soil* 223:119–132
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50
- Postma JA, Dathe A, Lynch JP (2014) The optimal lateral root branching density for maize depends on nitrogen and phosphorus availability. *Plant Physiol* 166:590–602
- Poulton PR, Johnston AE, White RP (2013) Plant-available soil phosphorus: part I: the response of winter wheat and spring barley to Olsen P on a silty clay loam. *Soil Use Manag* 29:4–11
- Rao IM, Fredeen AL, Terry N (1990) Leaf phosphate status, photosynthesis, and carbon partitioning in sugar beet. III. Diurnal changes in carbon partitioning and carbon export. *Plant Physiol* 92:29–36
- Richardson AE, Lynch JP, Ryan PR, Delhaize E, Smith FA, Smith SE, Harvey PR, Ryan MH, Veneklaas EJ, Lambers H, Oberson A, Culvenor RA, Simpson RJ (2011) Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant Soil* 349:121–156
- Ruan YL (2014) Sucrose metabolism: gateway to diverse carbon use and sugar signaling. *Ann Rev Plant Biol* 2014(65):33–67
- Rychter AM, Randall DD (1994) The effect of phosphate deficiency on carbohydrate-metabolism in bean. *Physiol Plantarum* 91:383–388
- Schmittgen TD, Livak KJ (2008) Analyzing real-time PCR data by the comparative C_T method. *Nat Protoc* 3:1101
- Shane MW, De Vos M, De Roock S, Lambers H (2003) Shoot P status regulates cluster-root growth and citrate exudation in *Lupinus albus* grown with a divided root system. *Plant Cell Environ* 26:265–273
- Shen J, Yuan L, Zhang J, Li H, Bai Z, Chen X, Zhang W, Zhang F (2011) Phosphorus dynamics: from soil to plant. *Plant Physiol* 156:997–1005
- Shi H, Wang B, Yang P, Li YB, Miao F (2016) Differences in sugar accumulation and mobilization between sequential and non-sequential senescence wheat cultivars under natural and drought conditions. *PLoS One* 11:e0166155. <https://doi.org/10.1371/journal.pone.0166155>
- Shipley B, Meziane D (2002) The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Funct Ecol* 16:326–331
- Silva-Navas J, Moreno-Risueno MA, Manzano C, Téllez-Robledo B, Navarro-Neila S, Carrasco V, Pollmann S, Gallego FJ, Del Pozo JC (2016) Flavonols mediate root phototropism and growth through regulation of proliferation-to-differentiation transition. *Plant Cell* 28:1372–1387
- Tang X, Ma Y, Hao X, Li X, Li J, Huang S, Yang X (2009) Determining critical values of soil Olsen-P for maize and winter wheat from long-term experiments in China. *Plant Soil* 323:143–151

- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol* 157:423–447
- Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecol Appl* 20:5–15
- Wang XR, Shen JB, Liao H (2010) Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crop? *Plant Sci* 179:302–306
- Wen ZH, Li HG, Shen JB, Rengel Z (2017) Maize responds to low shoot P concentration by altering root morphology rather than increasing root exudation. *Plant Soil* 416:377–389
- Wissuwa M, Gamat G, Ismail AM (2005) Is root growth under phosphorus deficiency affected by source or sink limitation? *J Exp Bot* 56:1943–1950
- Yang F, Huang S, Gao RC, Liu WG, Yong TW, Wang XC, Wu XL, Yang WY (2014) Growth of soybean seedling in relay strip intercropping systems in relation to light quantity and red: far-red ratio. *Field Crops Res* 155:245–253
- Zhang Y, Yu P, Peng Y, Li X, Chen F, Li C (2012) Fine root patterning and balanced inorganic phosphorus distribution in the soil indicate distinctive adaptation of maize plants to phosphorus deficiency. *Pedosphere* 22:870–877
- Zhang XR, Wang BM, Zhao YJ, Zhang JR, Li ZX (2019) Auxin and GA signaling play important roles in the maize response to phosphate deficiency. *Plant Sci* 283:177–188
- Zhou K, Yamagishi M, Osaki M, Masuda K (2008) Sugar signaling mediates cluster root formation and phosphorus starvation-induced gene expression in white lupin. *J Exp Bot* 59:2749–2756
- Zhou T, Wang L, Li S, Gao Y, Du Y, Zhao L, Liu W, Yang W (2019) Interactions between light intensity and phosphorus nutrition affect the P uptake capacity of maize and soybean seedling in a low light intensity area. *Front Plant Sci* 10. <https://doi.org/10.3389/fpls.2019.00183>
- Zhu J, Kaeppeler SM, Lynch JP (2005) Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays*). *Funct Plant Biol* 32:749–762
- Zhu J, Zhang C, Lynch JP (2010) The utility of phenotypic plasticity of root hair length for phosphorus acquisition. *Funct Plant Biol* 37:313–322
- Zobel RW, Kinraide TB, Baligar VC (2007) Fine root diameters can change in response to changes in nutrient concentrations. *Plant Soil* 297:243–254

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.