Short title: More crown roots improve phosphorus acquisition

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Large crown root number improves phosphorus acquisition in maize

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Summary: Maize genotypes with more crown roots have superior phosphorus acquisition, growth, and yield in low phosphorus soil.

Author contributions:

B.R.S. designed and conducted the experiments, analyzed the results, and led the writing; Y.Z.G. contributed to the design and writing; J.P.L. conceived and designed the study, supervised its execution, assisted with data analysis, and contributed to the writing.

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Abstract

We tested the hypothesis that maize genotypes with large crown root number (CN) will have shallower rooting depth and improved phosphorus (P) acquisition from low-P soils. Maize recombinant inbred lines with contrasting CN were evaluated under suboptimal P availability in greenhouse mesocosms and the field. Under P stress in mesocosms, the large-CN phenotype had 48% greater root respiration, 24% shallower rooting depth, 32% greater root length density in the topsoil, 37% greater leaf P concentration, 48% greater leaf photosynthesis, 33% greater stomatal conductance, and 44% greater shoot biomass than the small-CN phenotype. Under P stress in the field, the large CN phenotype had 32% shallower rooting depth, 51% greater root length density in the topsoil, 44% greater leaf P concentration, 18% greater leaf photosynthesis, 21% greater stomatal conductance, 23% greater shoot biomass at anthesis, and 28% greater yield than the small CN phenotype. These results support the hypothesis that large CN improves plant P acquisition from low-P soils by reducing rooting depth and increasing topsoil foraging. The large CN phenotype merits consideration as a selection target to improve P capture in maize and possibly other cereal crops.

Key words: Crown root number, phosphorus availability, maize, respiration, rooting depth, phosphorus capture.

Introduction

Maize (*Zea mays* L.) is a leading global crop, with importance for food security in developing nations (Grassini et al., 2013). Suboptimal phosphorus (P) availability is a primary limitation to plant growth in most agroecosystems (Lynch and Deikman, 1998; Vance et al., 2003; Lynch, 2007). In developing countries, most smallholder farmers cannot afford mineral fertilizer, and low soil P availability is a principal, pervasive constraint for crop production and therefore food security and economic development (Azeez et al., 2006; Worku et al., 2007). In developed countries, intensive P fertilization sustains high yields, but low utilization efficiency, limited reserves of high-grade phosphate ore deposits, high energy costs of producing fertilizer as well as environmental consequences of P effluents make intensive P fertilization unsustainable in the long term (Tilman, 2001; Zhang et al., 2008; Cordell et al., 2009). Therefore, developing cultivars with improved P acquisition is an important goal for global agriculture (Lynch, 2007).

The maize root system is composed of a primary root, a variable number of seminal roots, nodal roots arising from stem nodes, and lateral roots (Hochholdinger et al., 2004; Gao and Lynch, 2016). Crown roots are belowground nodal roots, and are primarily responsible for soil resource acquisition during vegetative growth and remain important through reproductive development (Hoppe et al., 1986; Hochholdinger et al., 2004; Lynch, 2013; Yu et al., 2014). Crown root number (CN), consisting of the number of belowground nodal whorls and the number of roots per whorl, is a central feature of maize root architecture and varies from five to 62 among maize genotypes (Bayuelo-Jiménez et al., 2011; Gaudin et al., 2011; (Bayuelo-Jiménez et al., 2011; Gaudin et al., 2011; Trachsel et al., 2011; Burton et al., 2013; Saengwilai et al., 2014b; York and Lynch, 2015; Gao and Lynch, 2016) Results from mesocosms and field studies showed that maize lines with small CN had greater nitrogen and water acquisition from deep soil strata under low nitrogen or drought conditions (Saengwilai et al., 2014b; Gao and Lynch, 2016). However, the utility of CN for P acquisition from P-limiting soils has never been tested, and is the focus of this study.

Phosphate is relatively immobile in soil, and P availability in surface soil strata is generally greater than that in subsoil strata, because of the deposition of plant residues over time and the greater biological activity in surface strata (Lynch and Brown, 2001; Lynch, 2011, 2013). Root phenes associated with enhanced topsoil foraging are therefore important for P acquisition (Lynch and Brown, 2001; Lynch, 2011; Richardson et al., 2011). Previous studies have shown that plants can improve P acquisition from low P soils through increased topsoil foraging, enabled by increased root length density (Manske et al., 2000) and lateral root branching (Desnos, 2008; Lynch, 2011), through shallow root growth angles (Lynch and Brown, 2001; Ho et al., 2005; Zhu et al., 2005), and through reduced root metabolic costs, such as the formation of root

cortical aerenchyma (Fan et al., 2003; Postma and Lynch, 2011a; Postma and Lynch, 2011b), root cortical senescence (Schneider et al., 2017), root hairs (Miguel, 2004; Lynch, 2011) and adventitious roots (Miller et al., 2003; Lynch and Ho, 2005). Axial roots, the primary structural framework of root systems, have particular importance in P acquisition (Lynch, 2011; Lynch, 2013). Results from greenhouse and field studies showed that common bean (*Phaseolus vulgaris*) with greater basal root whorl number had shallower rooting and greater root length, and thereby improved topsoil foraging, resulting in greater P acquisition and shoot biomass in low P soil (Lynch and Brown, 2012; Miguel et al., 2013). However, little information is available regarding how axial root number in Poaceae species responds to P stress and affects P capture.

Axial roots of annual dicot and monocot crop species have important differences that may affect the costs and benefits of axial root production for P capture. They are morphologically and developmentally distinct, as the majority of axial roots in monocots arise from shoot tissue, whereas axial roots in dicots consist primarily of the primary root and dominant lateral roots arising from it. For example, it was recently shown that the rate of secondary development in axial roots varies among genotypes of common bean (*Phaseolus vulgaris*), a dicot species, and that genotypes with reduced secondary development had greater P capture from low P soils (Strock et al., 2017). This adaptation to low P availability is not possible in monocot species, which lack secondary growth. The lack of secondary growth in monocots means that their axial roots are not as protected against biotic stress, which affects root longevity and therefore resource capture (Lynch, 2018). Because monocots lack secondary growth, their root cortical tissue is more persistent than in monocots, which has implications for P capture. For example, the formation of root cortical aerenchyma in axial roots is more advantageous for P capture in maize than in bean (Postma and Lynch, 2011a). Root cortical senescence may also increase P capture in monocot species (Schneider et al., 2017), but this process is not known to occur in dicots. The persistence of the root cortex also affects mycorrhizal symbioses, which are important for P capture, but require living cortex as habitat. Many dicot species have a dominant primary root, which with its laterals comprise the basic architectural phenotype. In contrast, in monocot species axial roots are continually produced from shoot nodes at or above the soil surface, which descend downward over time. These contrasting architectural strategies have important implications for the spatiotemporal dynamics of topsoil foraging and thereby for the acquisition of P, since the formation of new roots in dicots generally takes place as laterals of existing roots in deeper soil domains, which may have low P availability, whereas in monocots new roots form at or above the soil surface from shoot nodes, so that the topsoil is continuously explored throughout phenology. In addition, axial roots of monocot crops generally produce less root exudates capable of solubilizing P pools in the rhizosphere (Hinsinger et

al., 2011; Li et al., 2014), and have less mycorrhizal symbioses (Shen et al., 2011) than dicot crops. These factors can affect the costs and benefits of axial root production for P capture, resulting in different strategies to improve P acquisition. A survey of seven major crop species in response to P limitation found that monocots generally has morphological adaptations to P stress, while dicots, and especially legumes, primarily showed physiological adaptations to P stress, such as root exudate production (Lyu et al., 2016). Therefore, the utility of axial root number of Poaceae species for P capture in low P soil is uncertain, and whether the changes in axial roots production could improve topsoil exploration and thereby P acquisition and yield merits investigation.

The production of axial roots is a key element of root phenotypes, and is particularly important for the balance between the capture of mobile and immobile resources (Lynch, 2013). Results from mesocosms and the field showed that small CN was beneficial for nitrogen and water acquisition in conditions of suboptimal N or water availability Saengwilai et al., 2014b; Gao and Lynch, 2016). This can be attributed to the fact that the formation of a small number of crown roots can decrease interplant competition for soil resources, reduce metabolic costs and allocate extra metabolic resources for root elongation, thereby improving subsoil foraging for mobile resources like nitrogen and water, whose availability is greater in the subsoil in most agroecosystems (Saengwilai et al., 2014b; Lynch, 2015; Gao and Lynch, 2016). However, this may be disadvantageous for the capture of immobile soil resources like phosphorus, because of greater P bioavailability in shallow soil strata (Lynch, 2011; Lynch, 2013). On the other hand, production of a large number of crown roots can increase the sink strength of root systems, promote the development of root length and thereby improve soil resource acquisition, especially for P, whose acquisition mostly occurs <1 mm from the surface of a root and the intraplant and interplant competition is quite small (Nye and Tinker 1977; Varney and Canny, 1993; Miguel et al., 2013; Postma et al., 2014). Following the economic paradigm of plant resource allocation (Lynch and Ho, 2005), root construction and maintenance requires metabolic investment, which can exceed 50% of daily photosynthesis (Lambers et al., 2002). Thus, the metabolic costs of root construction and maintenance for a larger CN may potentially weaken the elongation of crown roots into deep soil strata and increase root distribution in surface soil strata (Gao and Lynch, 2016). While this may be disadvantageous for the capture of mobile soil resources like water and nitrogen (Saengwilai et al., 2014b; Zhan and Lynch, 2015; Zhan et al., 2015; Gao and Lynch, 2016), they will facilitate subsoil foraging for the immobile resources like P. Therefore, an intermediate number of crown roots may be ideal to co-optimize the mobile and immobile resources acquisition, and the optimum range of CN is likely to be greater in soils of low P availability (Lynch, 2013), although this hypothesis has not been tested empirically.

The objective of this study was to test the hypothesis that maize genotypes

with a large number of crown roots will have greater topsoil exploration, and therefore better P acquisition under suboptimal P availability, resulting in better plant growth and yield. To test this hypothesis, we compared the performance of maize recombinant inbred lines (RILs) sharing a common genetic background but having contrasting CN under contrasting P availability in greenhouse mesocosms and the field.

Results

Phosphorus stress effects on soil P availability

Phosphorus distribution in the mesocosms was stratified, and soil P availability (mg kg^{-1} dry soil) in the topsoil (0-20 cm) at 35 DAP was significantly greater than in the subsoil (20-140 cm), regardless of P regime. Compared to high P, P availability under low P was reduced by 92% in the topsoil and 64% in the subsoil (Fig. S2A). In the field, soil P availability at 0-10 and 10-20 cm was 42.7 and 21.9 mg kg^{-1} respectively under high P, and 7.3 and 4.4 mg kg^{-1} respectively under low P. No significant difference was found between high and low P treatments in the subsoil (20-60 cm) with soil P availability varying from 0.5 to 1.1 mg kg^{-1} (Fig. S2B).

Phosphorus stress effects on crown root number (CN)

Crown root number was significantly affected by P availability, phenotype and their interactions (Tables S1, S2). For both greenhouse and field experiments, CN, especially under high P, was significantly greater in large-CN phenotypes than in small-CN phenotypes (Fig. 1). When the comparison was done within each population, the large CN genotypes had significantly greater CN than the small CN genotypes under P deficiency, except IBM133 and NYH57 in the greenhouse and IBM133 and OHW170 in the field (Fig. S3). Phosphorus stress dramatically reduced CN for both phenotypes, by an average of 22% at 35 DAP in greenhouse mesocosms and 26% at anthesis in the field (Fig. 1). The effect of P availability on CN by nodal position differed in mesocosms and field conditions. In mesocosms, P stress did not influence the number of crown roots in the first, second and third nodes but significantly reduced the number of crown roots of the fourth, fifth and sixth nodes, and there was no sixth node development under P deficiency for either phenotype. The large-CN phenotype had significantly greater CN than the small-CN phenotype in the fifth node under both P regimes and in the sixth node under high P (Fig. 2A). In the field, CN of the third, fifth, sixth and seventh nodes of the large-CN phenotype was significantly reduced by P stress, while that of the small-CN phenotype was dramatically reduced from the second to the sixth node. Under high P, the small-CN phenotype had significantly less CN in the sixth node and no seventh node development relative to the large-CN phenotype; while under low P, CN of the small-CN phenotype was significantly less than that of the large-CN phenotype in the second and fourth nodes, and no seventh node developed for either phenotype (Fig. 2B).

CN effects on topsoil root length density and rooting depth

Under P deficiency, the large-CN phenotype proliferated more roots in the topsoil (mesocosms: 0-20 cm, by 32%; field: 0-10 cm, by 51%), and had shallower rooting depth (D_{75}, the depth above which 75% of total root length is located in the soil profile) by 24% in mesocosms and 32% in the field, as compared with the small-CN phenotype (Fig. 3B, D). However, there was no

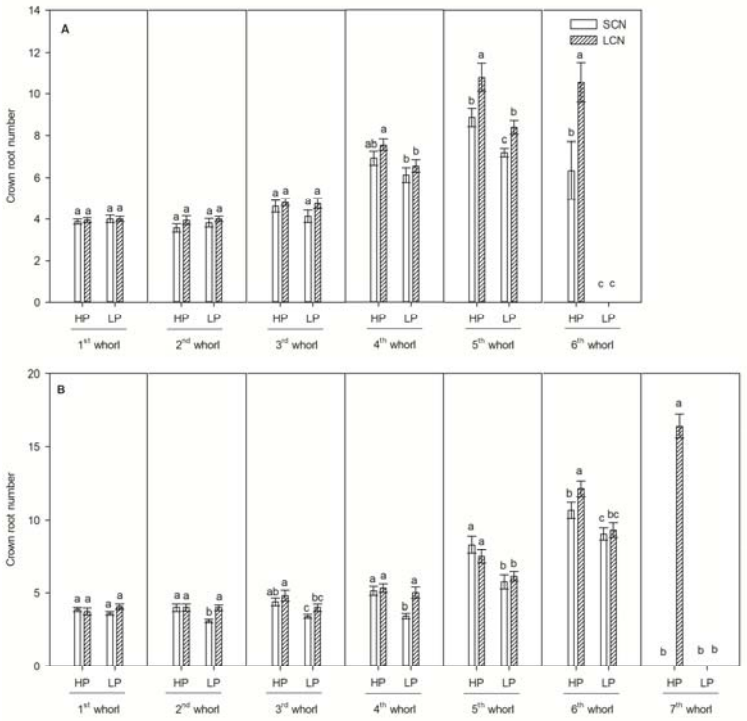

Fig. 2. Crown root number per node of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B) under high and low P. The data shown are means of four replications of four genotypes (± SE) in each phenotypic class of either large CN or small CN. Different letters represent significant differences ($P \leq 0.05$) compared within each node. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

significant difference between large and small CN phenotypes in topsoil root length density or D_{75} under high P (Fig. 3A, C). Under low P, CN was significantly associated with rooting depth (mesocosms: R^2 = 0.7762, P = 0.0038; field: R^2 = 0.6411, P = 0.0170) and root length density in the topsoil (mesocosms: R^2 = 0.6759, P = 0.0123; field: R^2 = 0.8579, P = 0.0009; Fig. 4).

CN effects on leaf photosynthesis and root respiration

Phosphorus availability, phenotype and their interactions had significant effects on leaf photosynthetic rate, stomatal conductance and root respiration (Tables S1, S2). Regardless of CN phenotype, P deficiency significantly reduced leaf photosynthetic rate, stomatal conductance and root respiration. Under low P, phenotypes with large CN had 48% (greenhouse) and 18% (field) greater leaf photosynthesis, 33% (greenhouse) and 21% (field) greater stomatal conductance, and 48% (greenhouse) greater root respiration than phenotypes with small CN. However, no significant difference was found between large-CN and small-CN phenotypes in leaf photosynthetic rate, stomatal conductance or root respiration under high P (Fig. 5).

CN effects on tissue P concentration, P acquisition and P acquisition efficiency

Leaf P concentration, plant P acquisition and P acquisition efficiency of both phenotypes were dramatically reduced by P stress (Tables S1, S2; Figs. 6, 8). Under P deficiency, P concentration, P acquisition and P acquisition efficiency of all large CN genotypes were significantly greater than that of small CN genotypes (Figs. S4 and S5), and the large CN phenotype had 37%

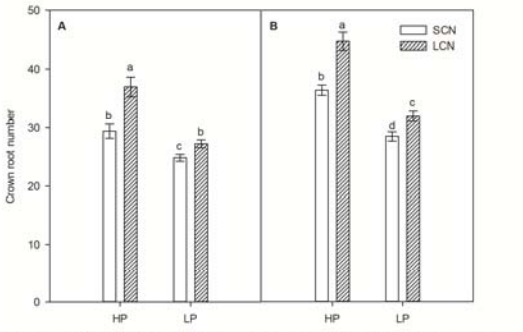

Fig. 1. Crown root number (CN) of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B) under high and low P. The data shown are means of four replications of four genotypes (± SE) in each phenotypic class of either large CN or small CN. Different letters represent significant differences compared within a panel at the level of α = 0.05. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

(greenhouse) and 44% (field) greater leaf P concentration, 97% (greenhouse) greater P acquisition, and 86% (greenhouse) greater P acquisition efficiency than phenotype with small CN (Tables S1, S2; Figs. 6, 8). Leaf P concentration (mesocosm: R^2 = 0.5796, P = 0.0282; field: R^2 = 0.5672, P = 0.0310), plant P acquisition (R^2 = 0.6105, P = 0.0220) and P acquisition efficiency (R^2 = 0.4834, P = 0.0556) under P deficiency were closely associated with CN (Figs. 7, 9). However, there was no significant difference between two phenotypes in leaf P concentration, P acquisition and P acquisition efficiency under high P (Figs. 6, 8).

CN effects on shoot biomass and grain yield

Phosphorus stress reduced shoot biomass and grain yield, and the reductions in the small-CN phenotype (shoot biomass: 51% in mesocosms and 35% in the field; yield: 46%) were greater than that in the large-CN phenotype (shoot biomass: 32% in mesocosms and 24% in the field; yield: 33%) (Tables S1, S2; Fig. 10). Under P deficiency, all large CN populations had greater shoot biomass and grain yield than the small CN populations (Fig. S6), and when the comparison was made between phenotypes, the large CN phenotype had 44% (greenhouse) and 23% (field) greater shoot biomass and 28% greater grain yield than the small CN phenotype (Tables S1, S2; Fig. 10). Both shoot biomass (mesocosm: R^2 = 0.5771, P = 0.0288; field: R^2 = 0.6068, P = 0.0227) and grain yield (R^2 = 0.7625, P = 0.0046) under P deficiency were closely associated with CN (Fig. 11).

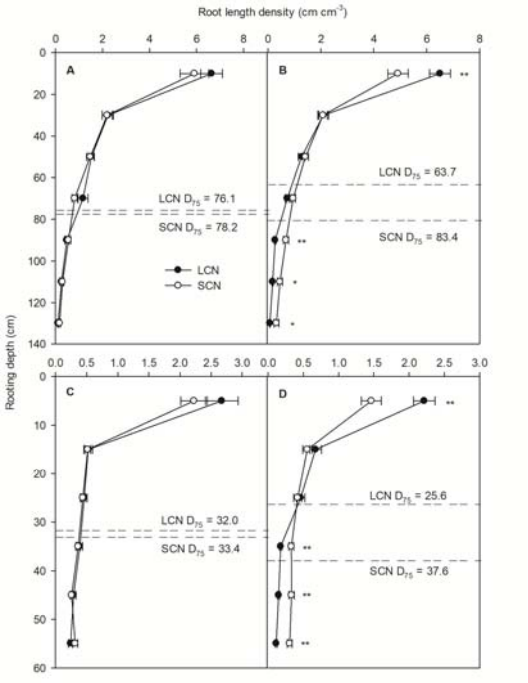

Fig. 3. Root length density (cm cm^{-3}) of maize at 35 DAP in greenhouse mesocosms under high phosphorus (A) and low phosphorus (B), and at anthesis in the field under high phosphorus (C) and low phosphorus (D). The data shown are means of four replications of four genotypes in each phenotypic category (± SE). The average values of D_{75} for four replications of four larger CN and four small CN genotypes are shown in each panel. *$P \leq 0.05$, **$P \leq 0.01$. LCN = large CN, SCN = small CN.

Discussion

Our results support the hypothesis that a large number of crown roots improves P acquisition by maize under P stress by increasing topsoil exploration (Figs. 3-4 and 6-9). Phenotypes differed in their CN under P stress (Figs. 1 and 2), lines with many crown roots had shallower rooting depth (Figs. 3 and 4), greater root length density in the topsoil (Figs. 3 and 4), greater P acquisition efficiency and P acquisition (Figs. 6-9), and therefore greater leaf photosynthesis and stomatal conductance (Fig. 5), biomass production, and yield (Figs. 10 and 11) than lines with few crown roots.

Lynch (2011) proposed that a greater number of axial roots may improve topsoil foraging and optimize P capture from low-P soils. Our results support the inclusion of large crown root number as an effective phene state for improved soil exploration and P acquisition under suboptimal P availability (Figs. 3-4, 6-9). We obtained comparable results from P stress treatments in two distinct environments, greenhouse mesocosms and the field. In the greenhouse, we used mesocosms to create P-stratified environments comparable to conditions in agricultural soils. Mesocosms are simplified, controlled environments, allowing detailed investigations of root physiological traits and root distribution by depth, since entire root systems can be easier excavated than the field study. The field experiment includes many environmental factors that may affect results. For example, mycorrhizal symbioses can increase P acquisition, extending soil exploration via the formation of mycorrhizal hyphae (Shen et al., 2011). The physical properties of

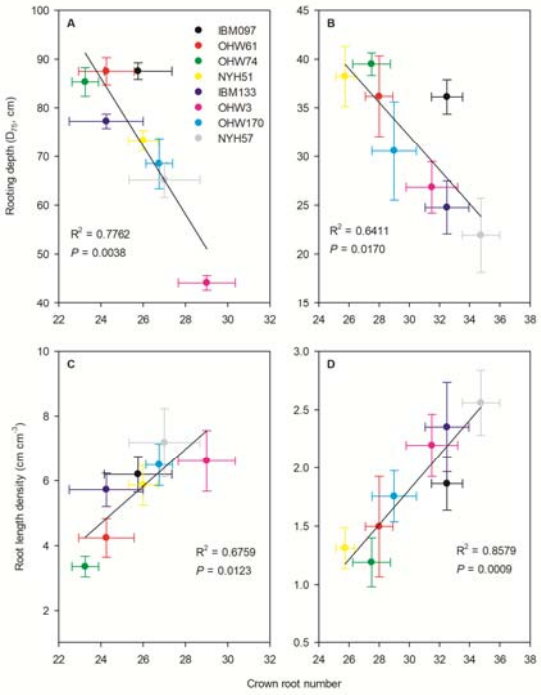

Fig. 4. Correlations between crown root number and rooting depth (D_{75}, cm) and root length density (cm cm^{-3}) from 0-20 cm soil depth of maize at 35 DAP in greenhouse mesocosms (A, C), and from 0-10 cm soil depth at anthesis in the field (B, D) under low phosphorus conditions. Each point is the mean of four replications of each genotype (± SE).

soil, such as impedance, structure, and texture, can independently or interactively influence root growth and thereby nutrient acquisition and yield production (Jin et al., 2013). We used RILs, which are particularly suited for the analysis of phenotypic traits governed by multiple genes, as is the case for CN in maize (Burton et al., 2014; Zhang et al. 2018). RILs within a population share a common genetic background (i.e. they descend from the same two parents) with no artificially induced mutations or transformation events, and the comparisons of several RILs from multiple populations enables the analysis of a phenotype in distinct genomes, which can minimize the risk of confounding effects from pleiotropy, epistasis, or other genetic interactions (Zhu and Lynch, 2004). Our results show that IBM133 and NYH57 in the greenhouse and IBM133 and OHW170 in the field had an intermediate CN under P deficiency (Fig. S3), but this did not substantially affect results: regardless of whether or not these genotypes were classified as having large CN, small CN, or were excluded entirely from the analyses, category means for large CN and small CN phenotypes under P deficiency were comparable for photosynthetic rate, stomatal conductance, root respiration, root length density in the topsoil, rooting depth, leaf P concentration, plant P acquisition, P acquisition efficiency, shoot biomass, and grain yield (Table S3). The fact that results from two distinct environments with 3 different sets of RILs are in agreement with each other is noteworthy and indicates that the utility of CN for P capture is independent of potentially confounding factors of any given environment and the specific genotypic context.

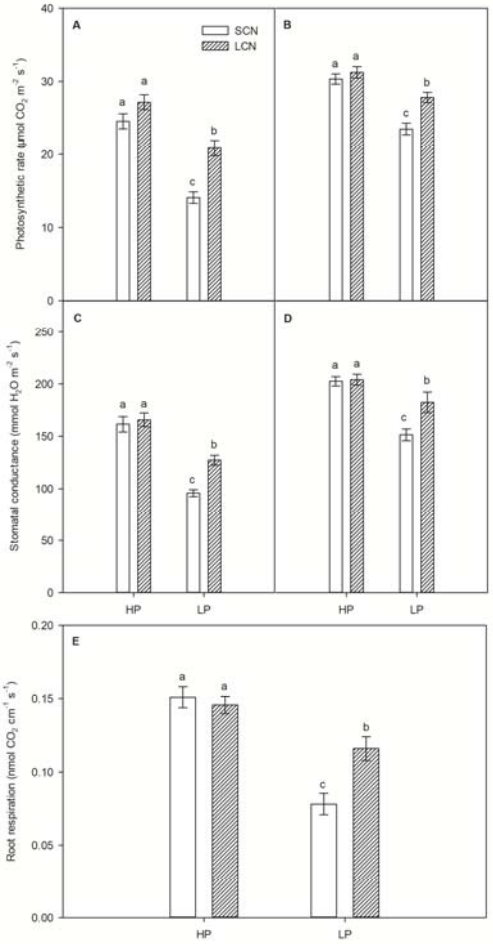

Fig. 5. Leaf photosynthesis (µmol CO_2 m^{-2} s^{-1}) and leaf stomatal conductance (mmol H_2O m^{-2} s^{-1}) of maize at 35 DAP in greenhouse mesocosms (A, C), at anthesis in the field (B, D) as well as root respiration (nmol CO_2 cm^{-1} s^{-1}) of maize at 35 DAP in greenhouse mesocosms (E) under high and low P. The data shown are means of four replications of four genotypes in each phenotypic category (± SE). Different letters represent significant differences compared within a panel at the level of α = 0.05. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Plant strategies to acquire P are oriented around two basic themes: soil exploration and mobilization of P from poorly available P pools in the rhizosphere (Lynch, 2011). Phosphorus mobilization mainly depends on the root-induced exudation of P mobilizing compounds, such as protons, organic acids and phosphatases (Hinsinger, 2001; Shen et al., 2011). Root architecture, the spatial configuration of the root system, determines the exploration and exploitation of localized P resources by the plant, the distribution of roots relative to their neighbors within and among root systems, as well as the placement and functional benefit of root exudates in specific soil domains, and is therefore particularly important for P acquisition (Lynch, 1995, 2011; Lynch and Brown, 2001; Miguel et al., 2013). In maize, crown roots are the majority of axial roots in the root system, contribute 60-80% of root biomass, and form the primary structural framework from which lateral roots emerge. The number of crown roots (CN), a central feature of maize root architecture, is an important regulator in soil resource capture by lateral roots and root symbionts (Lynch, 2013; Saengwilai et al., 2014b; Gao and Lynch,

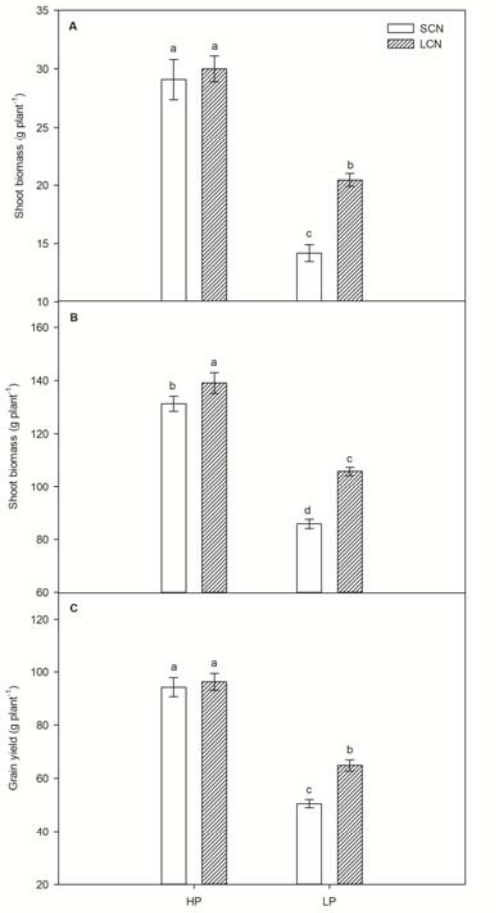

Fig. 10. Shoot biomass (g plant^{-1}) of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B), and grain yield (g plant^{-1}) at maturity in the field (C) under high and low P conditions. Data shown are means of four replications of four genotypes in each phenotype category ± SE. Different letters represent significant differences within a panel at the level of α = 0.05. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

2016).

The three primary soil resources that limit plant growth in most soils are N, P, and water. Water and N in the form of nitrate are highly mobile and tend to localize in deeper soil strata over time (Lynch and Wojciechowski, 2015; Thorup-Kristensen and Kirkegaard, 2016), whereas P is highly immobile and has greatest bioavailability in the topsoil (Lynch, 2011). It has previously been shown that reduced CN in maize is beneficial for the capture of water (Gao and Lynch, 2016) and N (Saengwilai et al., 2014b), by reducing the metabolic costs of soil exploration, resulting in greater rooting depth and thus greater capture of deep soil resources by remaining axial roots. The present data support the hypothesis that in contrast to water and N, P capture is improved by maize phenotypes with larger CN. This is a clear tradeoff: the optimal CN phenotype for P capture is opposite to the optimal CN phenotype for capture of water and N. Tradeoffs for the capture of mobile and immobile resources are evident for several root architectural phenes in maize. Shallow root growth angles favor topsoil foraging and P capture (Lynch, 2011), whereas steep root growth angles favor subsoil foraging and the capture of water (Ho *et al.*, 2005) and N

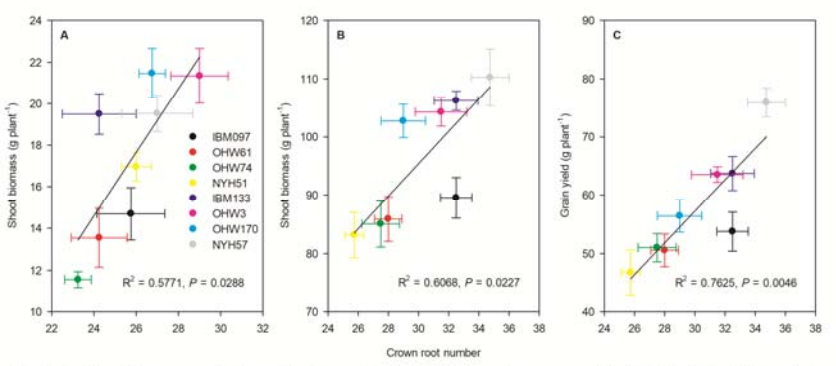

Fig. 11. Correlations between crown root number and shoot biomass of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B), and grain yield at maturity in the field (C) under low P conditions. Each point is the mean of four replicates of each genotype ± SE.

(Trachsel et al., 2013; Dathe et al., 2016). Dense lateral root branching promotes P capture (Postma *et al.*, 2014), whereas sparse lateral branching promotes the capture of water (Zhan *et al.*, 2015b) and N (Zhan and Lynch, 2015a). Anatomical phenes that reduce the volume of living cortical parenchyma, like RCA, RCS, and reduced CCFN, are beneficial for water capture but may reduce symbiotic P capture by reducing mycorrhizal habitat. Anatomical phenes that reduce the metabolic cost of soil exploration should have benefits for the capture of both mobile and immobile resources. For example, RCA is beneficial for the capture of the mobile resources water (Zhu et al., 2010; Chimungu et al., 2015) and N (Saengwilai et al., 2014a) while also being beneficial for the capture of the immobile resources P and K (Postma and Lynch, 2011a; Postma and Lynch, 2011b). Root hairs are useful for capture of P (Bates and Lynch, 2000a; Miguel et al., 2015) as well as water (Carminati *et al.*, 2017), while incurring little direct metabolic cost (Bates and Lynch, 2000b)) These tradeoffs in root form and function may account for the large phenotypic variation among crop genotypes, and suggest that for crop breeding programs, optimal root phenotypes should be identified for specific agroecologies (Lynch, 2018).

Results from greenhouse mesocosms and the field showed that root length density in the subsoil, where most water and nitrogen is distributed, was significantly increased under drought and nitrogen deficient conditions, resulting in improved water and nitrogen acquisition and plant growth (Zhan et al., 2015; Zhan and Lynch, 2015; Gao and Lynch, 2016). In the present study, the large-CN phenotype had 32% (greenhouse) and 51% (field) greater root length density in surface soil strata, where P availability is greatest, than the small-CN phenotype under P stress (Fig. 3 and Fig. 4), which dramatically increased topsoil exploration and thereby improved P acquisition, shoot biomass and grain yield (Fig. 6, Fig. 7, Fig. 8, Fig. 9, Fig. 10, Fig. 11).

Plants under P stress cannot simply grow more roots throughout the soil profile without regard for the costs of root growth and exploration (Lynch and Ho, 2005; Miguel et al., 2013, Lynch, 2015), but need to balance the metabolic allocations and tradeoffs among roots to optimize plant growth (Walk et al., 2006; Rubio and Lynch, 2007; Gao and Lynch, 2016). Walk et al. (2006) found

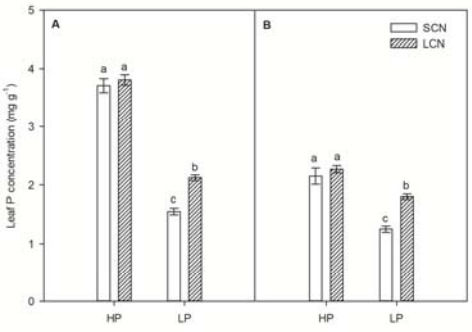

Fig. 6. Leaf P concentration (mg g^{-1}) of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B) under high and low P conditions. The data shown are means of four replications of four genotypes in each phenotype category ± SE. Different letters represent significant differences within a panel at the level of α = 0.05. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

that adventitious rooting of common bean (*Phaseolus vulgaris*) reduced the growth of tap and basal lateral roots, yet improved P acquisition by up to 10% in stratified soil. The removal of a specific root class induced an increase in the growth of the remaining root classes (Rubio and Lynch, 2007). In maize, under drought or nitrogen stress, reduced production of crown roots can conserve internal plant resources by reducing intra-plant root competition and metabolic costs, and thereby promote the remaining crown root axes to elongate rapidly, resulting in greater root depth, increased subsoil foraging for water or nitrogen and thus improved plant growth (Saengwilai et al., 2014b; Lynch, 2015; Gao and Lynch, 2016). In the present study, the large-CN phenotype had significantly more crown roots than small-CN phenotype under P stress, and the differences were mainly originated from fifth node in the greenhouse and from the second and fourth nodes in the field (Fig. 1 and Fig. 2), indicating that crown root number in later maturing nodes play crucial roles in plant P acquisition and yield production in late vegetative and reproductive growth. With increasing CN, the metabolic costs of root construction and maintenance was significantly greater (Fig. 5 and S7), and thus the resources available for axial root elongation were probably reduced (Lynch, 2013; Saengwilai et al., 2014b; Gao and Lynch 2016). Therefore, the large-CN phenotype had shallower rooting depth and less root length density in subsoil than the small-CN phenotype under P deficiency (Fig. 3 and Fig. 4).

Accumulating evidence indicates that plants with shallow rooting depth have growth advantages in P acquisition and yield production over deep-rooted cultivars under P stress (Lynch and Beebe, 1995; Bonser et al., 1996; Ge et al., 2000; Liao et al., 2001; Lynch and Brown, 2001; Ho et al., 2005; Zhu et al., 2005; Heppell et al., 2015), and topsoil foraging is one of the most important ways to improve plant fitness under suboptimal P availability (Lynch and Brown, 2001; Zhu et al., 2005; Lynch, 2011). In this study, results from both mesocosms and the field clearly showed that the shallowness of rooting depth of the large-CN phenotype was associated with improved P capture and thereby plant growth and yield in low P soils (Fig. 3, Fig. 4, Fig. 6, Fig. 7, Fig. 8, Fig. 9, Fig. 10, Fig. 11). Our results agree with previous studies which showed

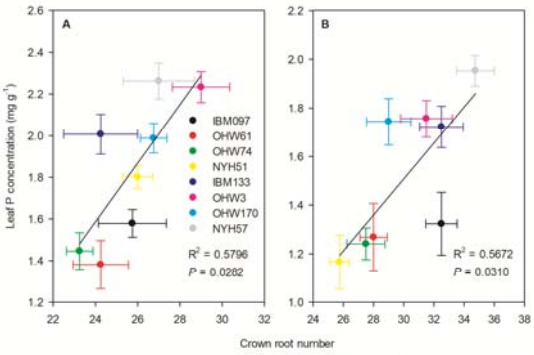

Fig. 7. Correlations between crown root number and leaf P concentration (mg g^{-1}) of maize at 35 DAP in greenhouse mesocosm (A), and at anthesis in the field (B) under low P conditions. Each point is means of four replicates of each genotype ± SE.

that the increased number of basal roots in common bean reduced internal resources available to individual basal root axes, slowed root elongation into deeper soil domains, and thus improved P acquisition and plant growth in low P soils (Walk et al., 2006; Rubio and Lynch, 2007; Miguel et al., 2013). Therefore, a large number of crown roots is a positive adaption to P stress in maize.

The rhizoeconomic paradigm indicates that plant fitness under water- and nutrient-limiting conditions is influenced by the balance between the benefits and the costs of root traits as direct metabolic costs, tradeoffs, opportunity costs and increased risks (Lynch and Ho, 2005; de Kroon and Mommer, 2006; Lynch, 2015), and the metabolic costs of root construction and maintenance are substantial (Lambers et al., 2002; Zhu et al., 2005). Previous studies have shown that reduced formation of crown roots can significantly reduce metabolic costs in root construction and maintenance, and more metabolic resources can be conserved for root elongation and water and nitrogen capture (Saengwilai et al., 2014b; Gao and Lynch 2016). However, in the case of suboptimal P availability, greater investment in axial root production slows axial root elongation, which is useful since P is immobile and enriched in the surface soil strata. As shown in the present study, although increased production of crown roots increased root respiration (Fig. 5 and Fig. S7), the large-CN phenotype was superior to the small-CN phenotype in adapting to P stress (Fig. 6, Fig. 7, Fig. 8, Fig. 9, Fig. 10, Fig. 11). Metabolic resources allocated to root growth and elongation into deep soil were significantly reduced, and root length density in the subsoil was decreased while that in the topsoil was significantly increased (Fig. 3 and Fig. 4), resulting in improved topsoil exploration and P acquisition (Fig. 8 and Fig. 9). Phosphorus is one of the important elements influencing photosynthesis, and P acquisition improvement can significantly increase net rate of photosynthesis, which is positively associated with the growth and yield of crop plants (Terry and Ulrich, 1973; Raghothama, 1999; Gastal and Lemaire, 2002). Therefore, the large-CN phenotype had substantially improved leaf photosynthesis, shoot biomass and grain yield, although the metabolic costs were increased (Fig. 5, Fig. 6, Fig. 7, Fig. 8, Fig. 9, Fig. 10, Fig. 11).

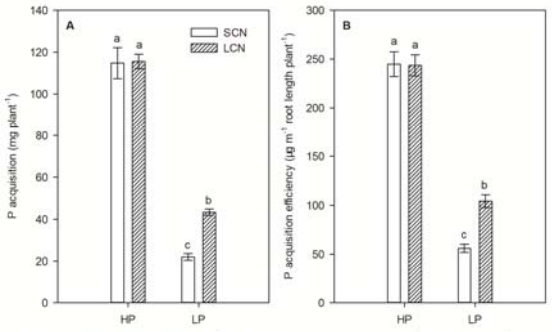

Fig. 8. Phosphorus acquisition (mg plant^{-1}) (A) and P acquisition efficiency (µg m^{-1} root length plant^{-1}) (B) of maize at 35 DAP in greenhouse mesocosms under high and low P conditions. The data shown are means of four replications of four genotypes in each phenotype category ± SE. Different letters represent significant differences within a panel at the level of α = 0.05. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

CN in maize varies greatly among genotypes and resource levels from five to 62 (Bayuelo-Jiménez et al., 2011; Gaudin et al., 2011; Trachsel et al., 2011; Burton et al., 2013; Saengwilai et al., 2014b; York et al., 2015; Gao and Lynch, 2016), and our range of CN (24-52) falls in the medium to high range of phenotypic variation observed. Moreover, CN is a heritable trait (Hetz et al., 1996; Burton et al., 2014), and genes affecting CN expression have been identified (Hetz et al., 1996; Taramino et al., 2007; Muthreich et al., 2013), making CN a feasible target for plant breeding. Although this study focused on maize, we suggest that the phenotype of large CN would improve P capture in other Poaceae species, e.g. sorghum, whose root system architecture is similar to that of maize (Lynch, 2013). Other graminaceous species such as wheat, rice, barley and oats have the same basic root structure as maize and may also benefit from the optimal CN, although greater density of nodal roots in tillering species may change the relationship of nodal root occupancy and resource capture. This merits investigation. Our results are entirely consistent with the hypothesis that large CN phenotype have shallower rooting depth and greater root length density in topsoil (Fig. 3 and Fig. 4), resulting in greater P acquisition from topsoil, improved growth and yield under P deficiency (Fig. 6, Fig. 7, Fig. 8, Fig. 9, Fig 10, Fig. 11). Therefore, we suggest that crown root number merits consideration as a potential trait to improve plants tolerance to P deficiency in crop breeding programs.

Materials and Methods

Plant materials

Eight genotypes of maize (*Zea mays* L.) were selected from three recombinant inbred line (RIL) populations, RILs IBM 133 and 097 from the intermated population of B73×Mo17 (IBM), and OHW3, 61, 74, and 170 from the RIL population of Oh43×W64a (OHW), and NYH 51 and 57 are from the RIL population of Ny821×H99 (NYH). Previous studies showed that these genotypes presented contrasting crown root number: IBM133, OHW3, OHW170 and NYH57 with large crown root number, and IBM097, OHW61, OHW74 and NYH51 with small crown root number (Bayuelo-Jiménez et al., 2011; Gaudin et al., 2011; Burton et al., 2013; Saengwilai et al., 2014b; York et

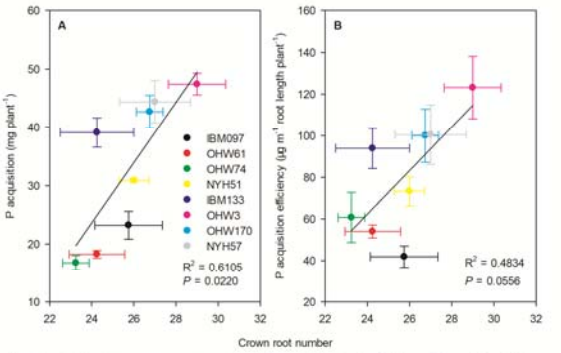

Fig. 9. Correlations between crown root number and P acquisition (mg plant^{-1}) (A) and P acquisition efficiency (µg m^{-1} root length plant^{-1}) (B) of maize at 35 DAP in greenhouse mesocosm under low P conditions. Each point is means of four replicates of each genotype ± SE.

al., 2015; Gao and Lynch, 2016). All seeds were obtained from Dr. Shawn Kaeppler (University of Wisconsin, Madison, WI, USA).

Greenhouse mesocosm study

Experimental design

The greenhouse experiment was a randomized complete block design. The factors were two phosphorus regimes (high and low phosphorus conditions), eight genotypes and four replications. Planting was staggered seven days between replicates with time of planting treated as a block effect.

Growth conditions

Plants were grown from May 16 to June 20 2016 in a greenhouse located on the campus of Pennsylvania State University in University Park, PA, USA (40°48′ N, 77°51′ W), with a photoperiod of 14/10 h at 28/24 °C (light/darkness), 1200 µmol photons m^{-2} s^{-1} maximum PAR, and 40-70% relative humidity. Seeds of uniform size were surface-sterilized in 0.05% NaOCl for 15 min and imbibed for 24 h in aerated 1 mM $CaSO_4$, then placed in darkness at 28 ± 1 °C for two days. Seedlings of similar size were transplanted to mesocosms consisting of PVC cylinders 15.7 cm in diameter and 155 cm in height. The cylinders were lined inside with plastic sleeves made of 4 mil (0.116 mm) transparent hi-density polyethylene film, which were used to facilitate root sampling. The growth medium consisted of (by volume) 50% medium size (0.5-0.3 mm) commercial grade sand, 30% horticultural size #3 vermiculite, 5% perlite and 15% sieved low P topsoil. The topsoil was collected from the Russell E. Larson Agricultural Research Center in Rock Spring, PA (Fine, mixed, semiactive, mesic Typic Hapludalf, pH 6.7, silt loam, P availability (Mehlich) 5.56 mg kg^{-1}). A uniform volume (29 L) of the mixture was used in each cylinder to ensure a consistent bulk density of the medium. Each cylinder was filled with medium to 5 cm from the surface and stratified into two layers, which were separated at 25 cm depth from the surface of the cylinder, with the upper layer 20 cm thick (5-25 cm depth) and the bottom layer 130 cm thick (25-155 cm depth). For the upper layer, phosphorus availability of the low and high phosphorus treatments was maintained at 60 ppm and 800 ppm,

respectively, by mixing the media with TSP (triple superphosphate, whose main component is $Ca(H_2PO_4)_2 \cdot H_2O$, with P content of about 20.1%) fertilizer; for the bottom layer, no phosphorus was applied in either phosphorus treatment.

One day before transplanting, each mesocosm was saturated with 4.0 L of a nutrient solution adjusted to pH 6.0 and consisting of (in μM): N (16000), K (6000), Ca (4000), S (1000), Mg (1000), Cl (50), B (25), Mn (2.0), Zn (2.0), Cu (0.5), Mo (0.5) and EDTA-Fe (50). Three plants were transplanted to each cylinder and thinned to one after 5 days. Following transplanting, plants were irrigated with 300 ml per mesocosm of the nutrient solution every two days for the first 10 days via drip irrigation using a DI-16 Dosatron fertilizer injector (Dosatron International Inc., Dallas, TX, USA), and 300 ml of nutrient solution was applied daily thereafter.

Sampling and measurements

Plants were harvested 5 weeks after transplanting. Two days before harvest, net photosynthesis rate of the youngest fully expanded leaf was measured with a Licor-6400 Infrared Gas Analyzer (Li-Cor Biosciences, Lincoln, NE, USA) using a red-blue light at PAR intensity of 1200 μmol photons m^{-2} s^{-1}, constant CO_2 concentration of 400 ppm, 25 °C leaf temperature, and 40% relative humidity.

The youngest fully expanded leaf was sampled and oven-dried. Tissue samples were ashed at 495 °C for 15 h, dissolved in 8 ml of 100 mM HCl and then analyzed for P concentration spectrophotometrically (Murphy and Riley, 1962). Shoots were severed at the soil surface, then oven-dried at 70 °C for 72 h for biomass determination. Roots were extracted by rinsing the media with water. All nodal roots emerging belowground were classified as crown roots. Crown root number in each nodal whorl was counted manually.

Root respiration of three 10-cm root segments from the second whorl of crown roots (8 cm from the base) was measured. Excised root samples were patted dry and placed in a 40 ml custom chamber connected to the Li-6400 IRGA. The temperature of the chamber was maintained at 25 ± 1°C using a water bath while respiration was measured. Carbon dioxide evolution from the root segments was recorded every 5 seconds for 180 seconds.

Root length distribution was measured by cutting the root system into 8 segments in 20 cm depth increments. Roots from each increment (preserved in 75% EtOH) were spread in a 5 mm layer of water in transparent plexiglass trays and imaged with a flatbed scanner equipped with top lighting at a resolution of 23.6 pixels mm^{-1} (600 dpi). Total root length for each segment was quantified using WinRhizo Pro (Regent Instruments, Québec, Canada). Following scanning the roots were dried at 70 °C for 72 h and weighed. To summarize the vertical distribution of the root length density we used the D_{75}, i.e. the depth above which 75% of the root length was located.

Field experiment

Growth conditions and experimental design

The field experiment was conducted during May to September in 2016 at the Russell E. Larson Agricultural Research Center of The Pennsylvania State University at Rock Spring, PA (40°43′N, 77°56′W). The soil was a Hagerstown silt loam (fine, mixed, mesic Typic Hapludalf). Based on soil analysis at the beginning of the cropping season, P fertilizers were applied at the rate of 78.5 kg P ha^{-1} for high-P plots, while low P plots received no P fertilizer. Other nutrients were adjusted to meet the requirements for maize production as determined by soil tests. Pest control and irrigation were carried out as needed.

A randomized complete block design with a split-plot arrangement of treatments was employed. The main plot was high and low P levels, and the subplot was treated with eight genotypes. There were four biological replications for each treatment. Each plot consisted of three rows, and each row had 18 plants grown with 0.76 m inter-row spacing and 0.23 m in-row spacing, resulting in a plant population of 57,000 plants ha^{-1}.

Sampling and measurements

Shoots and roots were harvested at anthesis (ca. 80 days after planting). Two days before harvest, net photosynthesis rate (Pn) of the ear leaf was measured as described above except PAR intensity was set to 1800 μmol photons m^{-2} s^{-1}, with a constant CO_2 concentration of 400 ppm, leaf temperature of 25 °C, and relative humidity of 40%.

Two adjacent plants were randomly selected in the central row per replicate. The ear leaves were sampled, oven-dried and then ground for tissue P analysis. Shoots were severed at the soil surface, oven-dried at 70 °C for 72 h before dry weight determination. Roots were excavated by removing a soil cylinder ca. 40 cm diameter and 25 cm depth with the plant base as the horizontal center of the soil cylinder. A large portion of soil was removed from roots by careful shaking. The remaining soil was removed by soaking the roots in diluted commercial detergent followed by vigorously rinsing with water. Because two representative root crowns within a plot usually appear to be homogeneous, only one clean root crown was selected for phenotyping. Crown root number in each nodal whorl was measured by counting.

Root distribution was measured by soil coring (Giddings Machine Co., Windsor, CO, USA). One soil core 5 cm diameter and 60 cm length were taken midway between plants within a row in each plot. Each soil core was subdivided into 10 cm segments, and roots were extracted from each segment and washed. Subsequently the washed roots were scanned with image processing software WinRhizo Pro (Regent Instruments, Québec, Canada) to obtain root length in each soil depths. Root distribution in the soil profiles was calculated as described above, and roots were then oven dried at 70 ^{o}C for 80 h, and dry

weight was determined.

At physiological maturity (ca. 127 days after planting), grain yield was collected from 6 plants per plot, and calculated at zero water content after drying at 75 °C for 100 h.

Data analysis

Statistical analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA). Normality and homogeneity of variances were tested for all the data with Shapiro-Wilk tests. Two-way ANOVA was used to assess the effects of high and low CN lines, P levels and their interactions, with block as a random factor. Duncan's multiple range test was used for multiple comparisons. Differences of soil P availability in the same soil depth between high P and low P and root length density in the same soil depth between high CN and low CN genotypes were analyzed by t-test. Linear regressions and correlations were carried out by Sigmaplot 12.5 (Systat Software Inc., CA, USA). Significance level was set at $P \leq 0.05$.

Acknowledgements

We thank Xucun Jia and Robert Snyder for technical assistance.

Figure legends

Fig. 1. Crown root number (CN) of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B) under high and low P. The data shown are means of four replications of four genotypes (± SE) in each phenotypic class of either large CN or small CN. Different letters represent significant differences compared within a panel at the level of $\alpha = 0.05$. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Fig. 2. Crown root number per node of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B) under high and low P. The data shown are means of four replications of four genotypes (± SE) in each phenotypic class of either large CN or small CN. Different letters represent significant differences ($P \leq 0.05$) compared within each node. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Fig. 3. Root length density (cm cm^{-3}) of maize at 35 DAP in greenhouse mesocosms under high phosphorus (A) and low phosphorus (B), and at anthesis in the field under high phosphorus (C) and low phosphorus (D). The data shown are means of four replications of four genotypes in each phenotypic category (± SE). The average values of D_{75} for four replications of four larger CN and four small CN genotypes are shown in each panel. *$P \leq 0.05$, **$P \leq 0.01$. LCN = large CN, SCN = small CN.

Fig. 4. Correlations between crown root number and rooting depth (D_{75}, cm) and root length density (cm cm^{-3}) from 0-20 cm soil depth of maize at 35 DAP in greenhouse mesocosms (A, C), and from 0-10 cm soil depth at anthesis in the field (B, D) under low phosphorus conditions. Each point is the mean of four replications of each genotype (± SE).

Fig. 5. Leaf photosynthesis (μmol CO_2 m^{-2} s^{-1}) and leaf stomatal conductance (mmol H_2O m^{-2} s^{-1}) of maize at 35 DAP in greenhouse mesocosms (A, C), at anthesis in the field (B, D) as well as root respiration (nmol CO_2 cm^{-1} s^{-1}) of maize at 35 DAP in greenhouse mesocosms (E) under high and low P. The data shown are means of four replications of four genotypes in each phenotypic category (± SE). Different letters represent significant differences compared within a panel at the level of $\alpha = 0.05$. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Fig. 6. Leaf P concentration (mg g^{-1}) of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B) under high and low P conditions. The data shown are means of four replications of four genotypes in each phenotype category ± SE. Different letters represent significant differences within a panel at the level of $\alpha = 0.05$. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Fig. 7. Correlations between crown root number and leaf P concentration (mg g^{-1}) of maize at 35 DAP in greenhouse mesocosm (A), and at anthesis in the field (B) under low P conditions. Each point is means of four replicates of each

genotype ± SE.

Fig. 8. Phosphorus acquisition (mg plant^{-1}) (A) and P acquisition efficiency (μg m^{-1} root length plant^{-1}) (B) of maize at 35 DAP in greenhouse mesocosms under high and low P conditions. The data shown are means of four replications of four genotypes in each phenotype category ±SE. Different letters represent significant differences within a panel at the level of $\alpha = 0.05$. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Fig. 9. Correlations between crown root number and P acquisition (mg plant^{-1}) (A) and P acquisition efficiency (μg m^{-1} root length plant^{-1}) (B) of maize at 35 DAP in greenhouse mesocosm under low P conditions. Each point is means of four replicates of each genotype ±SE.

Fig. 10. Shoot biomass (g plant^{-1}) of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B), and grain yield (g plant^{-1}) at maturity in the field (C) under high and low P conditions. Data shown are means of four replications of four genotypes in each phenotype category ± SE. Different letters represent significant differences within a panel at the level of $\alpha = 0.05$. HP = high P, LP = low P, LCN = large CN, SCN = small CN.

Fig. 11. Correlations between crown root number and shoot biomass of maize at 35 DAP in greenhouse mesocosms (A) and at anthesis in the field (B), and grain yield at maturity in the field (C) under low P conditions. Each point is the mean of four replicates of each genotype ± SE.

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