

Stimulated fine root growth benefits maize nutrient uptake under optimized nitrogen management

X. Zeng^a, Y. Peng^{b,c,*}

^aInstitute of Protected Agriculture, Chinese Academy of Agricultural Engineering, Beijing 100125, China.

^bKey Laboratory of Plant-Soil Interactions, MOE, Center for Resources, Environment and Food Security, College of Resources and Environmental Science, China Agricultural University, Beijing 100193, China.

^cState Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.

*Corresponding author. E-mail: pengyf@ibcas.ac.cn

Received 15 May 2016; Accepted after revision 31 July 2016; Published online 17 January 2017

Abstract

Optimized nitrogen (N) management reduces total N application without sacrificing crop yield. However, the underlining mechanisms have not been well investigated, especially lacking the evidence from roots. Here we performed a two-year field experiment with maize grown under zero-N, conventional N and optimized N applications and examined grain yield, N, phosphorous (P) and potassium (K) uptake and root length in diverse diameter classes. Results showed that both conventional N and optimized N managements significantly increased plant nutrient contents and grain yield compared with zero-N treatment, but no obvious difference was observed between the two N-fertilized treatments. Notably, the response of different nutrients to N application was not synchronous temporally over the growth period, following the order of N first, P second and K last. Though N application generally had minor impact on total root length and root biomass, optimized N regime significantly increased fine root (diameter ≤ 0.2 mm) length compared with conventional N at the eighth leaf emerged stage. The stimulated fine root growth under optimized N management is beneficial for adequate N uptake during the key growth stage, which determines subsequent PK acquisition and final crop yield. Our findings highlight the importance of fine roots in maize NPK uptake and a better understanding of the response of fine roots to changes in N availability may therefore be critical for optimizing N input in maize farming system.

Keywords: Root length; Phosphorous (P); Potassium (K); Leaf area; Grain yield; *Zea mays* L.

Introduction

Maize is one of the three most important food sources worldwide, reaching a total production of 1.02 billion tons in 2013 (FAO, 2015). Nitrogen (N) is generally recognized as a limiting nutrient in many agricultural systems (Marschner, 2011). N deficiency usually leads to decreases in leaf growth (i.e., both length and width) and photosynthetic rate of maize, thus reducing biomass accumulation and final grain yield (Uribelarrea et al., 2009; Ciampitti and Vyn, 2011; Peng et al., 2013a, 2014). In contrast, overuse of N not only has no benefit for grain yield, but also exerts negative impacts on environments, such as NO_3^- leaching and N_2O emission (Ju et al., 2009; Chen et al., 2014). Imbalanced N utilization occurs in both undeveloped and developing economies. Sometimes imbalance results from inputs that are insufficient to maintain soil fertility such as in sub-Saharan Africa. But other times, excessive and environmentally damaging surplus N occurs in many rapidly developing countries, such as China (Vitousek et al., 2009).

China has experienced a fast increase in grain production over the past decades, however, the cost of N fertilizer is much greater than the yields it produced in the same period (e.g., 71% increase in yield vs 271% increase N fertilizer cost, Ju et al., 2009). Furthermore, maize farmers in China usually apply all N fertilizer at one application usually before sowing and there is little top dressing at later growth stages (Peng et al., 2013b). Due to the NO_3^- leaching to the deeper soil and N_2O volatilization to atmosphere, this management system cannot supply adequate N for maize growth as N demand varied at different growing stages (Peng et al., 2012). During the past years, large efforts have been undertaken to optimize N management for reducing N application without sacrificing crop yield and the morphological and physiological mechanisms have also been examined (Ju et al., 2009; Rui et al., 2009; Peng et al., 2012, 2013b; Chen et al., 2014). Nevertheless, in field studies, very few researchers focused on maize roots in response to various N managements, though it is considered that roots play a dominant role in nutrient uptake and assimilation (Gewin, 2010). The lack of root research is possibly due to roots being tangled and buried underground thus requiring a labor intensive sampling process (Gewin, 2010; Peng et al., 2012).

To address this issue, we have previously raised an optimized N regime using appropriate amount of total N fertilizer and synchronizing maize N demand and soil N supply at key growth stages to maintain the maximum grain yield. Meanwhile, we compared total root length among different N managements and found that N deficiency caused an early decrease in the total root length at the rapid vegetative growth stage, possibly leading to the reduced final grain yield (Peng et al., 2012). However, there are still two issues that remain unexplored. First, except N, phosphorus (P) and potassium (K) are also important nutrients for plant growth (Marschner, 2011). Yet how different N managements influence maize P and K uptake has not been addressed. Second, it is unknown whether and how different sizes of roots respond to various N managements and how they impact maize nutrient uptake at different growth stages. For some tree and grass species, fine roots, rather than coarse roots, have a larger contribution to N uptake (Gower et al., 1992; Sullivan et al., 2000). Hence, it is necessary to examine root changes in different diameters classes under various N managements.

Here a two-year field study was performed with maize hybrid 'DH 3719' grown under three N regimes (no N, conventional N and optimized N). The 'DH 3719' is a stay-green maize cultivar popularly planted in North China. Grain yield and its two components (kernel number and weight) were measured at final harvest; leaf area was quantified at each node and ear-leaf (leaf subtending the ear) and chlorophyll content (indicated by Soil and Plant Analyzer Development, SPAD) was determined at tasseling; shoot dry weight, N, P and K contents, specific root length (root length per biomass) and root length in three diameter classes (≤ 0.2 mm, fine roots; 0.2-0.5 mm, medium roots; > 0.5 mm, coarse roots, Sullivan et al., 2000) were assessed at the eighth leaf emerged (V8), tasseling (VT) and grain blister stages (R²). The aims of this study are to: (i) examine the influences of various N managements on maize growth and N, P, and K uptake at different growth stages; (ii) compare root growth in different diameter classes under no N, conventional N and optimized N regimes.

Materials and Methods

Experimental Design

The field experiment was carried out at Shangzhuang Experimental Station of China Agricultural University, Beijing (40° N; 116° E) in 2008 and 2009. Two different,

adjacent sites were used each year in order to eliminate N accumulation and carryover from the previous year. The soil chemical properties (0-30 cm) in the two study sites were: mineral N (N_{\min} , $\text{NO}_3^- + \text{NH}_3^+$) 3.53 mg kg^{-1} and 6.78 mg kg^{-1} , Olsen-P 7.63 mg kg^{-1} and 7.14 mg kg^{-1} , NH_4OAc -extracted K 76.3 mg kg^{-1} and 97.6 mg kg^{-1} , organic matter 11.5 g kg^{-1} and 7.3 g kg^{-1} and pH 8.00 and 7.86. Maize hybrid 'DH 3719' was sown on 27 Apr. 2008 and 27 Apr. 2009 and harvested on 19 Sep. 2008 and 21 Sep. 2009, respectively. The seeds were sown with wide row (50 cm) and narrow row (20 cm) alternatively and the distance of two plants between intra-rows was 28 cm. Daily precipitation during the growing season each year is shown in Figure 1.

Three N treatments: 1) no N applied as control (N0); 2) conventional N practice (450 kg N ha^{-1} , Con.), based on a number of high-yield studies in China; 3) optimized N management (250 kg N ha^{-1} , Opt.), determined by plant N accumulation and soil N_{\min} at various stages in a preliminary experiment in the previous year, were imposed in a randomized complete block design with four replicates. The detailed rate and time of N fertilization are shown in Table 1. Other fertilizers, P (135 kg ha^{-1} of P_2O_5 as triple superphosphate) and K (120 kg ha^{-2} of K_2O as potassium sulfate) and zinc (30 kg ha^{-2} of $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$) were also applied to ensure no other nutrient limitations. N fertilizer was applied after plant sampling each time. Border plots were planted on the sides of the experimental field.

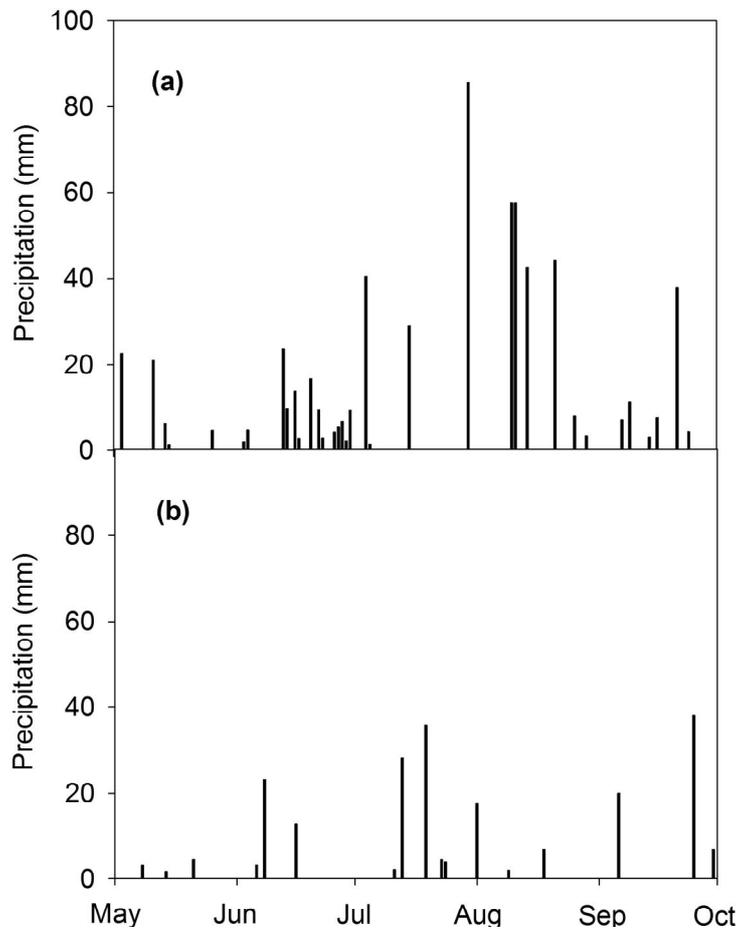


Figure 1. Daily precipitation during maize growing season in 2008 (a) and 2009 (b).

Table 1. N application rates and timing in the field experiments in 2008 and 2009.

Year	Treatment	Base fertilizer	V8	V12	VT	Total N (kg ha ⁻¹)
2008	N0	0	0	0	0	0
	Con.	175	50	170	55	450
	Opt.	60	120	70	0	250
2009	N0	0	0	0	0	0
	Con.	175	120	70	85	450
	Opt.	60	120	70	0	250

V8, the eighth leaf emerged; VT, tasseling stage; R², grain blister stage.

Measurement Protocols

Plants were sampled at V8, VT and R² stages in both years. At each harvest, six plants were cut at the stem base, killed at 105 °C and dried at 60 °C until weight stabilized and dry weights were determined. Then plant samples were chopped and ground into fine powder. Tissue N concentration was analyzed using a modified Kjeldahl digestion method (Nelson and Somers, 1973), P concentration was determined by molybdovanadate method (Soon and Kalra, 1995) and K concentration by a flame photometer using the remained digests. Plant N, P and K contents were calculated by multiplying their concentrations with dry weight. Grain yield was measured at physiological maturity, when 50% of the plants displayed black layer formation in the grains from the mid-portion of the ears. Ears in the central area of 14 m² (2008) and 21 m² (2009) within each plot were hand-harvested and weighted. Kernels from six randomly selected ears were shelled and moisture content and kernel percentage was calculated. Grain yield was estimated based on kernel percentage and expressed at 15.5% moisture content.

Maize leaf areas at individual nodes were determined according to Montgomery (1911). In each plot, six plants were labelled and the length and maximum width of leaves were measured when fully expanded and used to calculate the leaf area according to length×maximum width×0.75. Ear leaf chlorophyll content was assessed with a 502 Minolta SPAD meter (Spectrum Technologies, Inc., Plainfield, IL, USA) at VT stage. During each measurement, thirty plants were chosen randomly in each plot, the SPAD readings were taken from four equal distant spots from the base to the tip of the leaf blade. The mean value of the four readings from the 30 plants was calculated and used for data analyses.

After excision of the shoots at each harvest, two whole roots were collected and used to assess dry weight and N, P and K contents. In addition, we dug a soil block with a volume of 28 cm × 35 cm and a total depth of 50 cm in 2008 and a depth of 60 cm in 2009 in each plot of different treatments. All of the visible roots in the soil block were picked out and placed in individual marked plastic bags. These roots were washed free of soil after transfer to the laboratory and then analyzed for root length as described in Peng et al. (2010). Briefly, roots were scanned and saved as TIFF format, then the images were analyzed using the software WinRHIZO version 5.0 (Regent Instruments Inc, Quebec City, Canada). In the process of image analysis, roots were categorized into to 10 diameter classes with each 0.1 mm interval. We classified fine, medium and coarse roots as those diameters ≤ 0.2 mm, 0.2-0.5 mm and > 0.5 mm, respectively (Sullivan et al., 2000).

Statistical Analysis

Comparison of treatment difference was performed by analysis of variance (ANOVA) with the SAS package (SAS Institute, 2004). The Fisher's Protected Least

Significant Difference (FPLSD) test was used to separate treatment means which exhibited significant differences ($P < 0.05$).

Results

Influence of different N managements on maize grain yield, leaf traits and nutrient uptake

N applications significantly increased maize grain yield, kernel number per ear and 100-kernel dry weight compared with zero-N. No significant differences in yield or its components were observed between Con. and Opt. treatments (Table 2). Maize leaves located above eighth node were substantially smaller in no N treatment than those in Con. and Opt. treatments in 2009, while pronounced difference was only found in those leaves in the vicinity of the ear in 2008 (Figure 2a, b). Leaf chlorophyll content was greater with N fertilization in both years (Figure 2c, d).

Similar to grain yield, maize plant dry weight and N, P and K contents were significantly influenced by N application, but the responses of diverse nutrients were not synchronous temporally over the whole growth period (Tables 2, 3). Maize N uptake was sensitive to N application across all the three sampling stages, while obvious difference of plant P content was found at VT and R² stages, but difference of K was only significant at R² stage (Table 2).

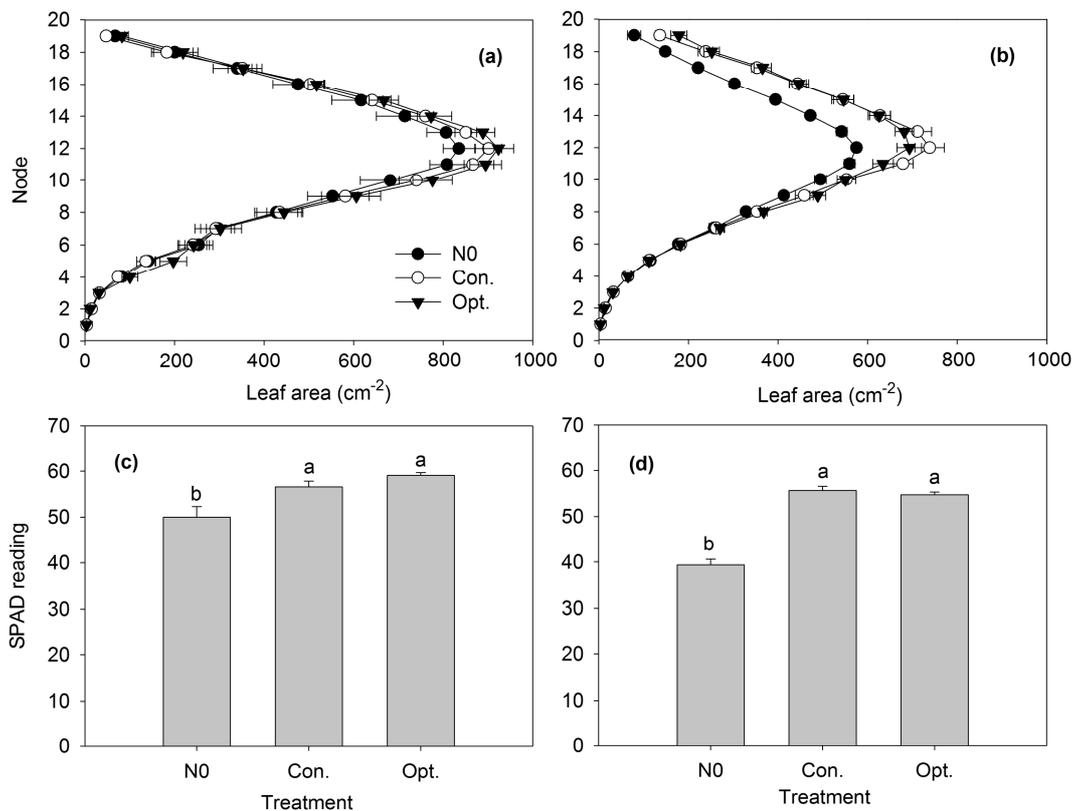


Figure 2. Maize leaf area at each node and ear-leaf SPAD reading at tasseling (a and c, respectively, in 2008; b and d, respectively, in 2009) under different N treatments. Bars denote the standard error of the mean (n = 4).

Table 2. Maize plant dry weight, 100-kernel dry weight, kernel number and grain yield response to different N managements in 2008 and 2009.

Year	Treatment	Plant dry weight (g plant ⁻¹)			100-kernel dry weight (g)	Kernel number	Grain yield (Mg ha ⁻¹)
		V8	VT	R ²			
2008	N0	13.6 ^{a†}	94.8 ^a	163.8 ^a	26.0 ^b	436 ^b	11.0 ^b
	Con.	14.9 ^a	98.5 ^a	176.1 ^{ab}	29.5 ^a	543 ^a	13.1 ^a
	Opt.	18.2 ^a	104.0 ^a	210.9 ^a	30.5 ^a	552 ^a	13.8 ^a
2009	N0	12.0 ^a	77.9 ^b	123.6 ^b	23.1 ^b	319 ^b	6.3 ^b
	Con.	13.8 ^a	110.0 ^a	206.1 ^a	26.2 ^a	495 ^a	11.0 ^a
	Opt.	13.0 ^a	102.9 ^a	194.9 ^a	26.4 ^a	491 ^a	10.7 ^a

† Means in columns in each year followed by a different letter represent a significant difference between N treatments (P<0.05). V8, the eighth leaf emerged; VT, tasseling stage; R², grain blister stage.

Table 3. Responses of maize whole plant N, P and K contents to different N managements in 2008 and 2009.

Year	Treatment	N content (g plant ⁻¹)			P content (g plant ⁻¹)			K content (g plant ⁻¹)		
		V8	VT	R ²	V8	VT	R ²	V8	VT	R ²
2008	N0	0.38 ^{b†}	1.11 ^b	1.51 ^b	0.04 ^a	0.14 ^b	0.25 ^b	0.25 ^a	1.16 ^a	1.44 ^b
	Con.	0.46 ^{ab}	1.73 ^a	2.04 ^{ab}	0.05 ^a	0.19 ^a	0.31 ^a	0.25 ^a	1.13 ^a	1.31 ^b
	Opt.	0.55 ^a	1.73 ^a	2.34 ^a	0.05 ^a	0.20 ^a	0.35 ^a	0.36 ^a	1.26 ^a	1.92 ^a
2009	N0	0.21 ^b	0.65 ^b	0.89 ^b	0.03 ^a	0.16 ^b	0.24 ^b	0.19 ^a	1.02 ^a	0.95 ^b
	Con.	0.33 ^a	1.70 ^a	2.14 ^a	0.04 ^a	0.22 ^a	0.35 ^a	0.22 ^a	1.18 ^a	1.45 ^a
	Opt.	0.27 ^a	1.47 ^a	1.98 ^a	0.04 ^a	0.19 ^{ab}	0.32 ^a	0.20 ^a	1.14 ^a	1.31 ^a

† Means in columns in each year followed by a different letter represent a significant difference between N treatments (P<0.05). V8, the eighth leaf emerged; VT, tasseling stage; R², grain blister stage.

Root growth in response to various N managements at different growth stages

N application generally had no significant influence on total root length at different growth stages, with exception of the V8 stage in 2009, when optimized N significantly increased total root length compared with conventional N treatment (Figure 3b). Similar to total root length, except that root biomass followed the trend as Con. > Opt. > N0 at VT stage in 2008, there was no significant difference among all treatments in root dry weight (Figure 3c). However, Opt. treatment had significant higher specific root length than Con. treatment at V8 stage in both years, possibly indicating that fine root growth was stimulated under optimized N management during this time.

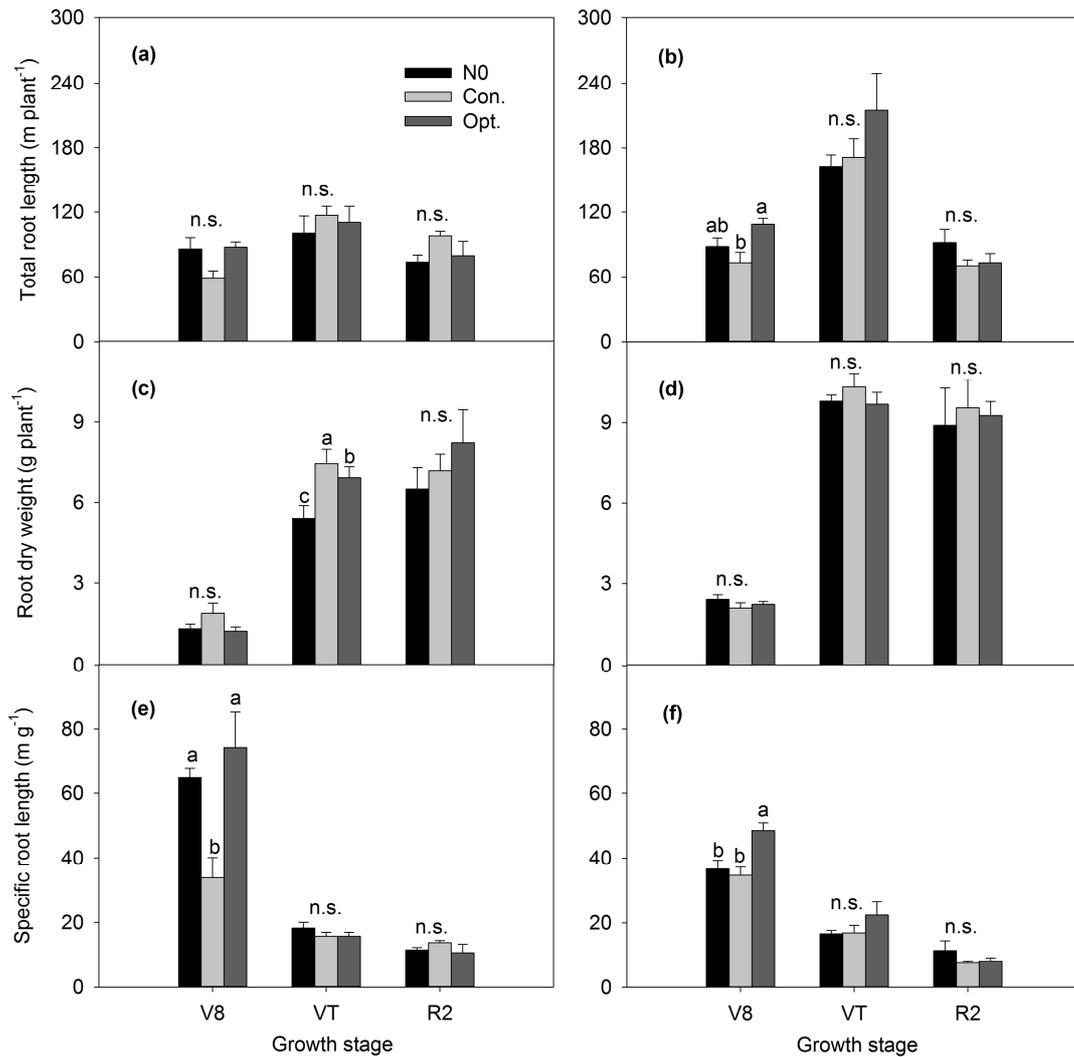


Figure 3. Maize total root length, root dry weight and specific root length (a, c and e, respectively in 2008; b, d and f, respectively in 2009) at V8 (the eighth leaf emerged), VT (tasseling) and R² (grain blister) stages under different N treatments. Bars denote the standard error of the mean (n = 4).

Further analysis of roots in different diameter classes indicated that, compared with Con. treatment, optimized N significantly increased the length of those roots ≤ 0.2 mm diameter in both years at V8 stage and this pattern was also observed for roots between 0.2-0.5 mm diameter in 2009 (Figure 4a, b). Yet, except VT stage in 2009 when roots > 0.5 mm diameter in Opt. treatment was greater than that in N0 treatment, there was no consistent, pronounced difference in fine, medium and coarse roots at VT and R² stages among different N treatments (Figure 4c-f).

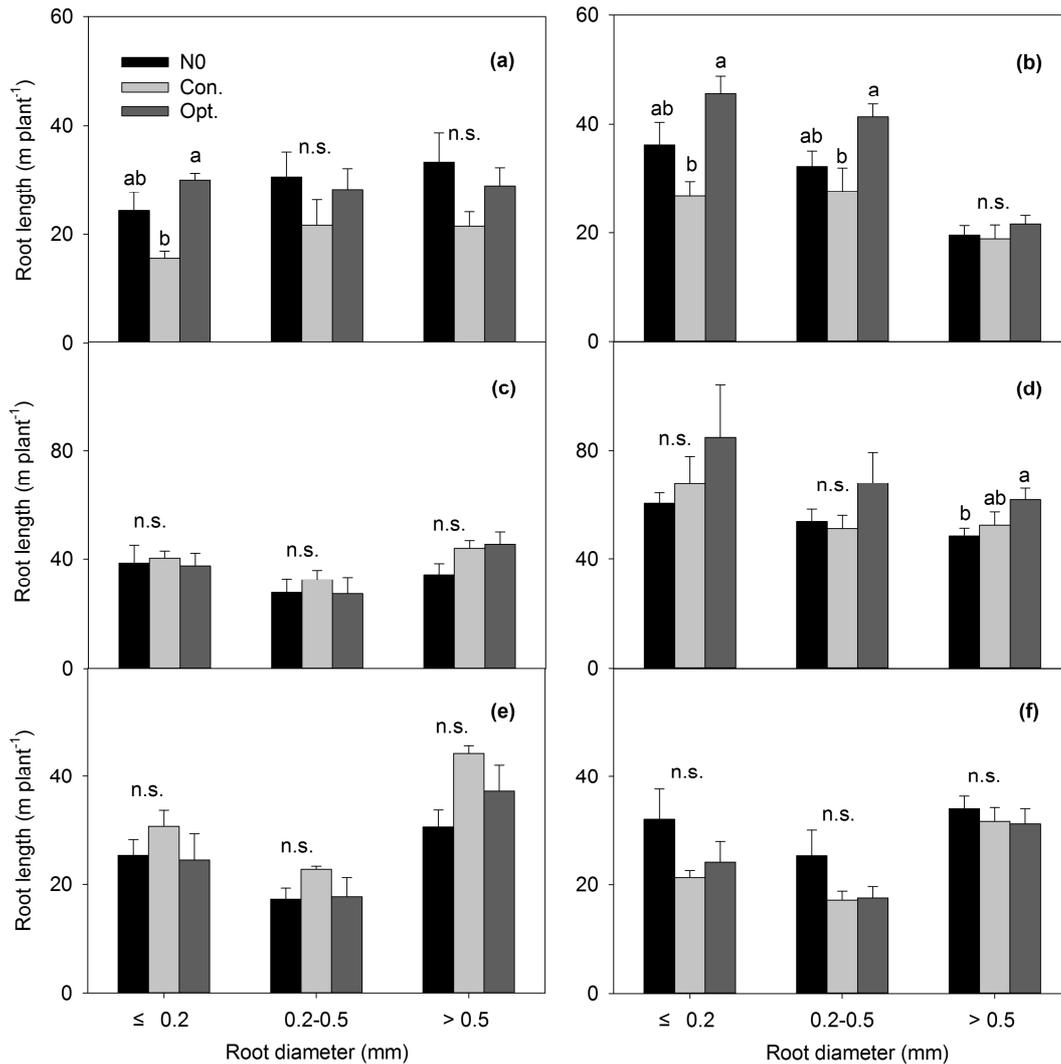


Figure 4. Maize root length in diverse diameter classes at V8, VT and R² (a, c and e, respectively, in 2008; b, d and f, respectively, in 2009) under different N treatments. Bars denote the standard error of the mean (n = 4).

Discussion

Optimized N management increased ear-stage fine root growth which benefits maize N uptake

Our study indicated that, in a maize planting system, the optimized N management reduced total N input by 44% compared to the conventional N practise (Table 1), but without reducing final grain yield (Table 2). This is presumably because optimized N application meets plant nutrient demands at different growth stages (Peng et al., 2012). The period between V8 and VT is recognized as the key stage for maize N uptake (Ciampitti et al., 2011). Grain yield was significantly reduced when inadequate N was supplied at this period (Subedi and Ma, 2005; Peng et al., 2012). In the current study, only about one-third base fertilizer was applied in Opt. treatment compared with Con. treatment (Table 1), but there was no significant difference of the N uptake between the two treatments at V8 stage (Table 3). This may be explained by the stimulated fine roots

under Opt. treatment up to the V8 growth stage. Fine roots are generally assumed to contribute more to plant N uptake due to their larger production, higher N concentration and greater turnover rate (Guo et al., 2004; Chen and Brassard, 2013). For instance, in Kentucky bluegrass, Sullivan et al. (2000) observed that fine roots (diameter ≤ 0.2 mm) were positively correlated with N uptake rate, while there was no correlations between coarser roots (diameter > 0.5 mm) and N uptake rate. We found that optimized N management significantly increased specific root length compared with conventional N at V8 stage (Figure 3e, f) indicating that maize plants under optimized N produce more root length using the same amount of carbon than conventional N management. Further analysis showed that optimized N mainly stimulated the length of those roots ≤ 0.2 mm diameter (Figure 4a, b). Enhanced fine root growth increases the absorbing surface resulting in adequate N uptake despite lower N application rates, thus possibly resulting in the similar N uptake, leaf area and chlorophyll content between conventional and optimized N regimes (Table 3; Figure 2). The enhanced fine root growth under Opt. management may be attributed to the increase in lateral roots compared with the other N treatments. Numerous studies found that medium N supply stimulates lateral root proliferation and elongation in maize, whereas, high soil N concentration and uptake would inhibit lateral root growth (Zhang et al., 1999; Ho et al., 2009; Yu et al., 2014). N status regulates these processes possibly by modulating auxin levels and nitrate sensors (e.g., CHL1) (Yu et al., 2014).

Soil moisture exerts substantial influences on maize root growth across years (Figures 3, 4). The longer root length in 2009, especially those ≤ 0.2 mm and 0.2-0.5 mm in diameter, may be attributed to the low water potential resulting from less precipitation throughout the growing season (608 mm in 2008; 216 mm in 2009). Some types of roots are able to continue elongation at low water potentials though the shoot growth is repressed (Sharp et al., 1988; Yamaguchi et al., 2010). This is considered an important strategy of plant adaptation to water limitation that helps to maintain sufficient plant water and nutrient supplies (Ober and Sharp, 2007). In order to absorb enough water and nutrients for plant growth and metabolism under drought, maize needs to increase root growth, possibly not only those ≤ 0.2 mm diameter, but also those between 0.2-0.5 mm.

Unsynchronized responses of maize N, P and K uptake to different N managements over the whole growth period

Albeit both conventional and optimized N treatments significantly increased maize N, P and K contents, it seems that the uptake response of different nutrients to N application were not synchronous temporally over the whole growth period, but followed the order of N first, P second and K last (Table 3). The asynchronous uptake of N, P and K is possibly related to their demands, functions and distributions in plants. N is the mineral element that plants require in the greatest amounts and it serves as a constituent of many cell components, including amino acids, nucleic acids and enzymes (Taiz and Zeiger, 2010). Therefore, under N enrichment, maize plants may need to acquire sufficient N to maintain high production of photosynthates for new tissue formation across the entire growth period. Plants generally take up less than one-tenth P compared with N, although P is also an important component of plant cells. However, P is mainly distributed in reproductive organs in maize (Ning et al., 2013) and hence, maize may not need to absorb an equivalent proportion of P to N at vegetative stage. K

plays an important role in cell osmotic potential regulation (Taiz and Zeiger, 2010) and plants also require a large amount of K. Nevertheless, since K is very mobile and can be translocated between various tissues (Marschner, 2011), maize K uptake may not be as sensitive as N and P at vegetative and early reproductive stages.

Though maize plants under conventional and optimized N treatments acquired more P and K than those in the N0 treatment at reproductive stages, root length of all classes was generally insensitive to N treatments during this period (Figure 4c-f). Potentially this results are because when maize plant progresses to reproductive stages, most newly produced photosynthates are translocated to growing sink organs and thus less carbohydrates are allocated to roots. Therefore, root length may be less responsive to changes in soil N availability at later growth stages. However, the increase in root nutrient uptake activity rather than variation in root length may be dominant in regulating nutrient absorption from soil. Using three N levels, Chen et al. (2015) found that, albeit N application did not significantly affect maize total root length, the transport rates of N compounds in the xylem were considerably increased under N fertilizations during grain-filling stage. Therefore, they speculated that the overall root N-uptake rate should be enhanced in N treated maize.

Notably, the N rates for the Con. treatment slightly differed at growth stages between years (Table 1). These changes were made because Con. treatment did not significantly increase maize grain yield compared with Opt. treatment in 2008 and we inferred that the N application rate (50 kg ha^{-1}) at V8 stage might be insufficient for maize growth in Con. treatment, since the V8 is considered as a key N uptake stage (Peng et al., 2012). Therefore, the same amount of N fertilizer was applied at V8 and V12 stages in both N treatments in 2009, to test whether more N fertilization at V8 stage could further increase maize yield for Con. treatment. However, no significant increase in maize grain yield was observed (Table 2), possible because the soil N_{\min} concentrations in Con. treatment were all higher than the critical N_{\min} at various stages in both years (see Peng et al., 2013b). Generally, maize yield would not be further increased when soil N_{\min} was above the critical N_{\min} concentration (Peng et al., 2013b). Thus we may conclude that the different N rate timing of the Con. treatment between 2008 and 2009 should have minor impact on the results and conclusions.

In summary, our study indicates that optimized N management reduced total N application while maintaining maize grain yield and nutrient uptake. This possibly resulted from the stimulated fine root growth at key growth stages. Meanwhile, the response of different nutrients to N application was not synchronous temporally. Obvious difference of maize N uptake among different N treatments was observed at all three sampling stages, while significant difference of plant P content was found at VT and R² stages and K uptake was only sensitive to N application at R² stage. These findings suggest that appropriate amount of N fertilizer as base fertilizer could enhance maize fine root growth at early stage, which is beneficial for sufficient nutrient acquisition over the whole growth period, thus maintaining the maximum grain yield. Given that previous studies usually examined total root length of maize in response to soil N changes (Wiesler and Host, 1993; Niu et al., 2010; Peng et al., 2012; Chen et al., 2015; Yu et al., 2015), future efforts are necessary to assess how different N managements affect fine root dynamics, rather than total roots, to improve N use efficiency in maize.

Acknowledgment

We thank the National Natural Science Foundation of China (31400417), China Postdoctoral Science Foundation (2014T70140 and 2013M540160) for financial support.

References

- Chen, H.Y.H., Brassard, B.W., 2013. Intrinsic and extrinsic controls of fine root life span. *Crit. Rev. Plant Sci.* 32, 151-161.
- Chen, X.P., Cui, Z.L., Fan, M.S., Vitousek, P., Zhao, M., Ma, W.Q., Wang, Z.L., Zhang, W.J., Yan, X.Y., Yang, J.C., Deng, X.P., Gao, Q., Zhang, Q., Guo, S.W., Ren, J., Li, S.Q., Ye, Y.L., Wang, Z.H., Huang, J.L., Tang, Q.Y., Sun, Y.X., Peng, X.L., Zhang, J.W., He, M.R., Zhu, Y.J., Xue, J.Q., Wang, G.L., Wu, L., An, N., Wu, L.Q., Ma, L., Zhang, W.F., Zhang, F.S., 2014. Producing more grain with lower environmental costs. *Nature*. 514, 486-489.
- Chen, Y.L., Zhang, J., Li, Q., He, X.L., Su, X.P., Chen, F.J., Yuan, L.X., Mi, G.H., 2015. Effects of nitrogen application on post-silking root senescence and yield of maize. *Agron. J.* 107, 835-842.
- Ciampitti, I.A., Vyn, T.J., 2011. A comprehensive study of plant density consequences on nitrogen uptake dynamics of maize plants from vegetative to reproductive stages. *Field Crops Res.* 121, 2-18.
- FAO FAOSTAT – Agriculture Database.
- Gewin, V., 2010. An underground revolution. *Science*. 466, 552-553.
- Gower, S.T., Vogt, K.A., Grier, C.C., 1992. Carbon dynamics of rocky mountain Douglas-fir: Influence of water and nutrient availability. *Eco. Monogr.* 62, 43-65.
- Guo, D.L., Mitchell, R.J., Hendricks, J.J., 2004. Fine root branch orders respond differently to carbon source-sink manipulations in a longleaf pine forest. *Oecologia*. 140, 450-457.
- Ho, C.H., Lin, S.H., Hu, H.C., Tsay, Y.F., 2009. CHL1 functions as a nitrate sensor in plants. *Cell*. 138, 1184-1194.
- Ju, X.T., Xing, G.X., Chen, X.P., Zhang, S.L., Zhang, L.J., Liu, X.J., Cui, Z.L., Yin, B., Christie, P., Zhu, Z.L., Zhang, F.S., 2009. Reducing environmental risk by improving N management in intensive Chinese agricultural systems. *P. Natl. Acad. Sci. USA*. 106, 3041-3046.
- Marschner, P., 2011. *Mineral Nutrition of Higher Plants*, 3rd edition. Academic Press, London.
- Montgomery, E.G., 1911. Correlation studies in corn. *Nebraska Agr. Exp. Sta. Annu. Rep.* 24, 108-159.
- Nelson, D.W., Somers, L.E., 1973. Determination of total nitrogen in plant material. *Agron. J.* 65, 109-112.
- Ning, P., Li, S., Yu, P., Zhang, Y., Li, C.J., 2013. Post-silking accumulation and partitioning of dry matter, nitrogen, phosphorus and potassium in maize varieties differing in leaf longevity. *Field Crops Res.* 144, 19-27.
- Niu, J.F., Peng, Y.F., Li, C.J., Zhang, F.S., 2010. Changes in root length at the reproductive stage of maize plants grown in the field and quartz sand. *J. Plant Nutr. Soil Sci.* 173, 306-314.
- Ober, E.S., Sharp, R.E., 2007. Regulation of root growth responses to water deficit. In: Jenks, M.A., Hasegawa, P.M., Jain, S.M. (Eds.), *Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops*. Springer, Dordrecht, pp. 33-53.
- Peng, Y.F., Li, C.J., Fritschi, F.B., 2013a. Apoplastic infusion of sucrose into stem internodes during female flowering does not increase grain yield in maize plant grown under nitrogen limiting conditions. *Physiol. Plant.* 148, 470-480.
- Peng, Y.F., Li, C.J., Fritschi, F.B., 2014. Diurnal dynamics of maize leaf photosynthesis and carbohydrate concentrations in response to differential N availability. *Environ. Exp. Bot.* 99, 18-27.
- Peng, Y.F., Li, X.X., Li, C.J., 2012. Temporal and spatial profiling of root growth revealed novel response of maize roots under various nitrogen supplies in the field. *PLoS ONE* 7, 37726.
- Peng, Y.F., Niu, J.F., Peng, Z.P., Zhang, F.S., Li, C.J., 2010. Shoot growth potential drives N uptake in maize plants and correlates with root growth in the soil. *Field Crops Res.* 115, 85-93.
- Peng, Y.F., Yu, P., Li, X.X., Li, C.J., 2013b. Determination of the critical soil mineral nitrogen concentration for maximizing maize grain yield. *Plant Soil.* 372, 41-51.
- Rui, Y.K., Peng, Y.F., Wang, Z.R., Shen, J.B., 2009. Stem perimeter, height and biomass of maize (*Zea mays* L.) grown under different N fertilization regimes in Beijing, China. *Int. J. Plant Prod.* 2, 85-90.

- Sharp, R.E., Davies, W.J., 1989. Regulation of growth and development of plants growing with a restricted supply of water. In: Jones, H.G., Flowers, T.L., Jones, M.B. (Eds.), *Plants Under Stress*. Cambridge University Press, London, pp. 71-93.
- Sharp, R.E., Silk, W.K., Hsiao, T.C., 1988. Growth of the maize primary root at low water potentials. I. Spatial distribution of expansive growth. *Plant Physiol.* 87, 50-57.
- Soon, Y.K., Kalra, Y.P., 1995. A comparison of plant tissue digestion methods for nitrogen and phosphorus analyses. *Can. J. Soil Sci.* 75, 243-245.
- Subedi, K.D., Ma, B.L., 2005. Nitrogen uptake and partitioning in stay-green and leafy maize hybrids. *Crop Sci.* 45, 740-747.
- Sullivan, W.M., Jiang, Z.C., Hull, R.J., 2000. Root morphology and its relationship with nitrate uptake in Kentucky bluegrass. *Crop Sci.* 40, 765-772.
- Taiz, L., Zeiger, E., 2010. *Plant Physiology*, 5th Ed. Sinauer Associates Inc., Sunderland, MA.
- Uribelarrea, M., Crafts-Brandner, S.J., Below, F.E., 2009. Physiological N response of field-grown maize hybrids (*Zea mays* L.) with divergent yield potential and grain protein concentration. *Plant Soil.* 316, 151-160.
- Vitousek, P.M., Naylor, R., Crews, T., David, M.B., Drinkwater, L.E., Holland, E., Johnes, P.J., Katzenberger, J., Martinelli, L.A., Matson, P.A., Nziguheba, G., Ojima, D., Palm, C.A., Robertson, G.P., Sanchez, P.A., Townsend, A.R., Zhang, F.S., 2009. Nutrient imbalances in agricultural development. *Science.* 324, 1519-1520.
- Wiesler, F., Horst, W.J., 1993. Differences among maize cultivars in the utilization of soil nitrate and the related losses of nitrate through leaching. *Plant Soil.* 151, 193-203.
- Yamaguchi, M., Valliyodan, B., Zhang, J., LeNoble, M.E., Yu, O., Rogers, E.E., Nguyen, H.T., Sharp, R.E., 2010. Regulation of growth response to water stress in the soybean primary root. I. Proteomic analysis reveals region-specific regulation of phenylpropanoid metabolism and control of free iron in the elongation zone. *Plant Cell Environ.* 33, 223-242.
- Yu, P., Li, X., White, P.J., Li, C., 2015. A large and deep root system underlies high nitrogen-use efficiency in maize production. *PLoS ONE.* 10, 126-293.
- Yu, P., White, P.J., Hochholdinger, F., Li, C.J., 2014. Phenotypic plasticity of the maize root system in response to heterogeneous nitrogen availability. *Planta.* 240, 667-678.
- Zhang, H.M., Jennings, A., Barlow, P.W., Forde, B.G., 1999. Dual pathways for regulation of root branching by nitrate. *P. Natl. Acad. Sci. USA.* 96, 6529-6534.