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Contribution of Root Proliferation in Nutrient-Rich Soil Patches to Nutrient Uptake and Growth of Maize*[1]

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ABSTRACT

Root proliferation can be stimulated in a heterogeneous nutrient patch; however, the functions of the root proliferation in the nutrient-rich soil patches are not fully understood. In the present study, a two-year field experiment was conducted to examine the comparative effects of localized application of ammonium and phosphorus (P) at early or late stages on root growth, nutrient uptake, and biomass of maize (*Zea mays* L.) on a calcareous soil in an intensive farming system. Localized supply of ammonium and P had a more evident effect on shoot and root growth, and especially stimulated fine root development at the early seedling stage, with most of the maize roots being allocated to the nutrient-rich patch in the topsoil. Although localized ammonium and P supply at the late stage also enhanced the fine root growth, the plant roots in the patch accounted for a low proportion of the whole maize roots in the topsoil at the flowering stage. Compared with the early stage, fine root length in the short-lived nutrient patch decreased by 44%–62% and the shoot dry weight was not different between heterogeneous and homogeneous nutrient supply at the late growth stage. Localized supply of ammonium and P significantly increased N and P accumulation by maize at 35 and 47 days after sowing (DAS); however, no significant difference was found among the treatments at 82 DAS and the later growth stages. The increased nutrient uptake and plant growth was related to the higher proportion of root length in the localized nutrient-enriched patch. The results indicated that root proliferation in nutrient patches contributed more to maize growth and nutrient uptake at the early than late stages.

Key Words: biomass, growth stage, intensive farming system, localized nutrient supply, root length

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INTRODUCTION

In natural environments, soil resources vary at a range of scales in spatial and temporal traits. In order to adapt to such large-scale resource heterogeneity, plant roots display remarkable plasticity in physiology and morphology to effectively capture nutrient resources (Drew, 1975; Robinson, 1994; Hodge, 2004, 2006; Weligama *et al.*, 2008; Jing *et al.*, 2010). The most common plasticity in root morphology is the increased root length (Drew, 1975; Hodge *et al.*, 1999; Zhang *et al.*, 1999). In root physiological plasticity, increased ion uptake capacity is very important for nutrient acquisition, and the nutrient uptake rate can be increased by three folds when roots encounter a nutrient-rich patch (Robinson, 1994).

Fine roots play a major role in nutrient-patch exploitation. They have the rapid turnover rate and can be deployed into patches to capture the nutrient resources (Campbell *et al.*, 1991; Jing *et al.*, 2010). Some evidence suggests that fine roots have the short life-span and high root respiration, and there is a strong relationship between root respiration and N concentration in fine roots (Reich *et al.*, 1998; Tjoelker *et al.*, 2005). In addition, fine roots have high nutrient uptake capacity, but may be less efficient because of the short life-span. However, the maintenance costs of fine roots may decline with time, resulting in a high efficiency of nutrient uptake in the long term (Bouma *et al.*, 2001; Hodge, 2006). Based on the cost-to-benefit ratio, rapid development of fine roots in short-lived nutrient patches (localized peaks of nutrient concentration lasting no more than 4 weeks) with short life-span may contribute to efficient root foraging for nutrient resources.

The root foraging response is defined as the plas-

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tic alteration in morphology and physiology of roots to enhance the capture of resources (Hutching and Kroon, 1994). The most important theory of foraging is marginal value theorem (MVT) (Charnov, 1976; Nonacs, 2001; McNickle and Cahill, 2009). As predicted by MVT, plants may invest more carbon energy into the nutrient-rich patches than homogeneous soil in terms of increasing root biomass or root-length density (Gleeson and Fry, 1997).

In our previous study, localized application of ammonium plus phosphorus (P) significantly induced root proliferation and increased maize growth and nutrient accumulation at the early growth stage (39 days after sowing, jointing) (Jing *et al.*, 2010). The positive effect on maize growth declined at the late stage (51 days after sowing, ten-leaf stage) because ammonium in the localized patches was gradually depleted with time *via* crop uptake as well as nitrification. The roots at the early and late growth stages may differ in responses to localized application of ammonium plus P. However, the root responses to the localized application of ammonium plus P and the corresponding contribution of root proliferation in the nutrient-rich patches to nutrient accumulation and plant growth throughout the growth cycle in maize are not fully understood even though such responses are very important in managing roots and rhizosphere for improved nutrient-use efficiency and crop growth. The objectives of the present study were to explore i) how to take full advantage of root foraging to improve plant growth and nutrient accumulation in the field and ii) whether there is a match between optimal root foraging and root distribution in the nutrient-rich soil patches at the early and late growth stages.

MATERIALS AND METHODS

A field experiment was carried out to test the effects of localized supply of P combined with ammonium on maize root foraging in nutrient patches in an intensive farming system in North China in 2009–2010. The experimental site was located at the research station of China Agricultural University in Shangzhuang, North China. The rainfall was 216 and 314 mm during the maize growing season in 2009 and 2010, respectively.

The soil was a silt loam with a bulk density of 1.44 g cm^{-3}, pH of 7.86 (1:5 soil:water suspension), organic carbon of 7.27 g kg^{-1}, available N of 36 mg kg^{-1}, Olsen-P of 4.3 mg kg^{-1}, and available K of 102 mg kg^{-1} in the topsoil layer (0–30 cm). In 2009, the plant density was controlled at 100 000 hills ha^{-1}, and the plants were arranged in alternating 20-cm- and 50-cm-wide rows (Fig. 1a) (Jing *et al.*, 2010). In 2010, the plant density changed to 67 500 hills ha^{-1}, and the plants were arranged in alternating 30-cm- and 60-cm-wide rows, with one plant per hill (Fig. 1b). Each treatment had four replicates in a completely randomized block design. The plot size was 5.6 m × 10 m. There were four fertilizer treatments established just before sowing in 2009 (N as ammonium sulphate and P as superphosphate): 1) both N and P broadcast (N_BP_B), 2) localized application of P and N (N_LP_L), 3) localized application of N and half-strength P before sowing as the first localized application along the mid-point line in narrow gap and the second localized application of N and half-strength P again at 55 days afte sowing (DAS) along the mid-point line in the wide row (D-N_LP_L), and 4) localized application of P and N as the N_LP_L treatment but with application rate of P decreased by one third (67% P_L+N_L). The localized nutrients were applied as follows: 1) A ditch (10-cm deep) was dug along the mid-point line in the narrow row, and the depth was 10 cm from the soil surface; 2) fertilizer was placed at the bottom of the ditch; and 3) the ditch was filled with soil. The localized fertilization site was 10 cm from the plant row along the mid-point line in the narrow row; for the D-N_LP_L treatment, the second localized application of N and half-strength P was done along the mid-point line in the wide row at 55 DAS (Fig. 1).

The application rates of fertilizers in each treatment at sowing in 2009 were as follows: 60 kg N ha^{-1} (as ammonium sulphate), 59 kg P ha^{-1} (as superphosphate) (29.5 kg P ha^{-1} in the D-N_LP_L treatment and 39.5 kg P ha^{-1} in the 67% P_L+N_L treatment), 66.4 kg K ha^{-1} (as potassium chloride), and 3.4 kg Zn ha^{-1} (as $ZnSO_4{\cdot}7H_2O$). At the jointing stage, the whole trial was top-dressed with 120 kg N ha^{-1} except for the D-N_LP_L treatment (60 kg ha^{-1} N in the D-N_LP_L treatment). At the eight-leaf stage, each treatment was top-dressed with 70 kg N ha^{-1} and 33.2 kg K ha^{-1}, and additional localized application of N was 60 kg ha^{-1} and P 29.5 kg ha^{-1} to complement the nutrient in the D-N_LP_L treatment. The same applications were conducted in 2010, except for the 67% P_L+N_L treatment.

To assess root distribution, an auger sampling method was used. Soil cores (10 cm diameter × 15 cm depth) were collected in the narrow row, plant row, and wide row (Fig. 1) in three depths at 15-cm increments (0–15, 15–30, and 30–45 cm). Whole roots in each sample were washed with water, and the root length was measured by a scanner and the WinRhizo software (Re-

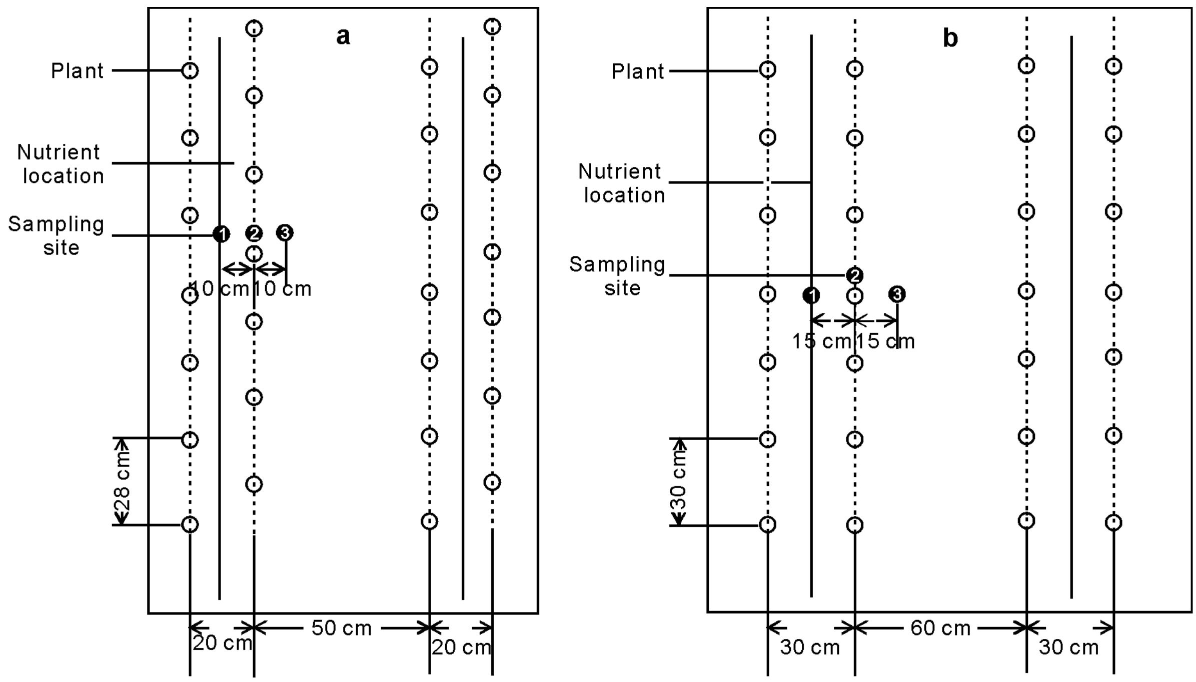

Fig. 1 Planting patterns and soil core sampling sites for maize seedlings in the field plots in 2009 (a) and 2010 (b). Distances between rows and plants are indicated in cm. The dotted lines represent planting rows. The open circles indicate planting sites. Closed circles with numbers represent the soil core sampling sites. The localized nutrients were applied along the mid-point line in narrow rows (solid lines).

gent Instruments Inc., Canada).

Plants were sampled (four plants per plot) at different growth stages: seedling (35 DAS in 2009 and 33 DAS in 2010), jointing (47 DAS in 2009 and 44 DAS in 2010), ten-leaf (65 DAS in 2009 and 62 DAS in 2010), flowering (82 DAS in 2009 and 75 DAS in 2010), and grain-filling (112 DAS in 2009 and 103 DAS in 2010) stages. Leaf area was calculated till the flowering stage by measuring leaf length and width according to Sanderson *et al.* (1981): leaf area = leaf length $\times$ maximum width $\times$ k, where k is a shape factor with a value of 0.5 for partially unfolded leaves and 0.75 for completely unfolded leaves. Chlorophyll content in the youngest fully developed leaves was assessed with a chlorophyll meter (SPAD-502, Minolta, Japan).

Analysis of variance was conducted using the SAS statistical software (SAS, 2001). Significant difference among means was determined by least significant difference (LSD) test at the $P \leq 0.05$ probability level.

RESULTS

Plant growth

Localized ammonium and P supply had a positive effect on plant growth including chlorophyll content, total leaf area, and plant biomass at different growth stages. The chlorophyll content in the youngest fully-developed leaves was measured at 33, 65, and 82 DAS (Table I). Compared with the N_BP_B (N broadcast and P broadcast supply) treatment, the chlorophyll reading was significantly higher in the treatments with localized ammonium and P supply (N_LP_L, D-N_LP_L, and 67% P_L+N_L) at 33 DAS. Even at 65 DAS, the differences between the N_BP_B and N_LP_L treatments and between the N_BP_B and 67% P_L+N_L treatments were also observed, but no significant difference was found at 82 DAS (flowering) among the treatments.

The positive effect on the total leaf area (LA) was also observed with localized supply of ammonium and P (Table II). Compared with the N_BP_B treatment, LA in the N_LP_L and D-N_LP_L treatments increased by 25% and 21%, respectively, but the effect disappeared at 75 DAS. There was no difference in LA between the N_LP_L and D-N_LP_L treatments throughout the whole maize growth period. The same trend was obvious for the leaf expansion rate (Fig. 2). In comparison to the N_BP_B treatment, the leaf expansion rate was higher in the N_LP_L and D-N_LP_L treatments at 33 and 44 DAS. No difference was observed at 62 and 75 DAS.

Shoot dry weights of maize were significantly higher in the N_LP_L and D-N_LP_L treatments than the N_BP_B treatment at 33 and 44 DAS in 2010 (Table II), and there were no differences among the treatments at 62 DAS and the later stages. In 2009, the shoot dry

TABLE I

Chlorophyll contents in the youngest fully-developed leaves and shoot dry weights of maize plants at different growth stages in 2009

Chlorophyll content[a)] or Shoot dry weight	Growth stage (days after sowing)	Treatment[b)]			
		N_BP_B	N_LP_L	D-N_LP_L	67% P_L+N_L
SPAD reading	Seedling (33)	48.7±0.9[c)] b[d)]	53.0±1.7 a	53.2±0.8 a	53.2±0.7 a
	Ten-leaf (65)	51.1±0.9 b	53.2±0.5 a	52.2±0.9 ab	54.0±0.4 a
	Flowering (82)	54.4±0.8 a	53.6±1.0 a	55.6±1.2 a	53.6±1.6 a
Shoot dry weight ($g\ plant^{-1}$)	Seedling (35)	5±0 b	7±1 a	7±1 a	5±0 b
	Jointing (47)	10±1 b	14±1 ab	14±2 ab	15±1 a
	Ten-leaf (63)	57±5 b	68±2 ab	78±4 a	68±3 ab
	Flowering (82)	90±6 a	108±6 a	109±2 a	107±4 a
	Grain-filling (112)	197±13 a	203±14(a)	206±20 a	200±14 a

[a)]Chlorophyll content was expressed as the stability of soil plant analytical development (SPAD) reading with a chlorophyll meter.
[b)]N_BP_B: N and P broadcast; N_LP_L: localized N and P supply; D-N_LP_L: double (localized application at 0 and 55 days after sowing) localized N and P supply; 67% P_L+N_L: localized 67% P and N supply.
[c)]Mean ± standard error of four replicates.
[d)]Means followed by the the same letter(s) in each row are not significantly different between treatments at a specific growth stage ($P \leq 0.05$).

TABLE II

Total leaf area (LA) and shoot dry weight of maize plants at different growth stages in 2010

Item	Treatment[a)]	Growth stage (days after sowing)				
		Seedling (33)	Jointing (44)	Ten-leaf (62)	Flowering (75)	Grain-filling (103)
Total leaf area ($cm^2\ plant^{-1}$)	N_BP_B	517±42[b)] b[c)]	2 552±125 b	5 489±148 b	7 285±164 a	6 347±190 a
	N_LP_L	644±49 a	2 883±135 a	5 929±159 a	7 438±70 a	6 529±33 a
	D-N_LP_L	626±32 a	2 876±109 a	5 914±183 a	7 404±120 a	6 438±174 a
Shoot dry weight ($g\ plant^{-1}$)	N_BP_B	3.7±0.4 b	12±1 b	87±17 a	111±2 a	233±12 a
	N_LP_L	6.0±0.6 a	20±1 a	95±16 a	119±5 a	247±15 a
	D-N_LP_L	5.7±0.4 a	23±2 a	92±4 a	117±2 a	251±7 a

[a)]N_BP_B: N and P broadcast; N_LP_L: localized N and P supply; D-N_LP_L: double (localized application at 0 and 55 days after sowing) localized N and P supply.
[b)]Mean ± standard error of four replicates.
[c)]Means followed by the the same letter(s) in each column are not significantly different between treatments at a specific growth stage for a specific item ($P \leq 0.05$).

weight exhibited a similar trend (Table I).

Compared with the N_BP_B and 67% P_L+N_L treatments, localized supply of ammonium and P in the N_LP_L and D-N_LP_L treatments significantly increased N (Fig. 3a) and P accumulation (Fig. 3b) by maize at 35 DAS in 2009. Even at 47 DAS, N and P accumulation was higher in the D-N_LP_L treatment than the N_BP_B treatment. However, no significant difference in N and P accumulation by maize was found among the treatments at 82 DAS and the later growth stages. The total amounts of N and P accumulation significantly increased with the duration of plant growth till 112 DAS.

Root length and distribution

Localized ammonium plus P supply stimulated root proliferation in the soil where the nutrients were locally applied (N_LP_L, D-N_LP_L, and 67% P_L+N_L treatments). The root-length density at the depths of 0–15 and 15–30 cm in the N_LP_L treatment was significantly greater than that in the N_BP_B treatment at 35 and 47 DAS (Fig. 4a, b). At 35 and 47 DAS, localized supply of only 67% P plus ammonium (67% P_L+N_L) and 50% P with ammonium (before the second application of ammonium and 50% P in the D-N_LP_L treatment) also stimulated root growth (0–15 cm layer) in the localized zone where ammonium and P were applied, with the root-length density being significantly higher than that in the N_BP_B treatment. No difference in the root-length density was observed between the N_LP_L, D-N_LP_L, and 67% P_L+N_L treatments at the soil depth of 0–15 cm. There was also no significant difference in the root-length density among the treatments at 30–45 cm depth. The similar effects of ammonium plus P in the N_LP_L and D-N_LP_L treatments in stimulating root proliferation were obtained in 2010.

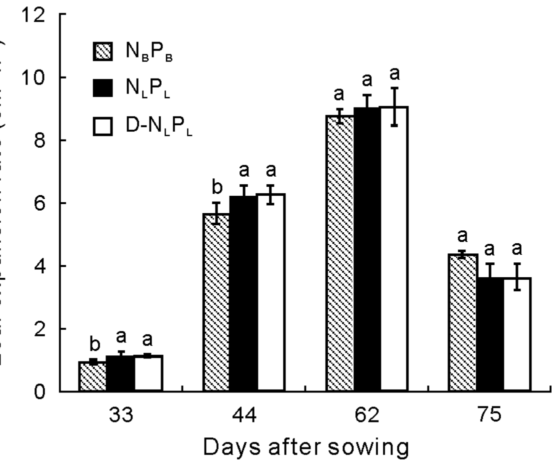

Fig. 2 Effects of different nutrient treatments on leaf expansion rates of maize plants at 33 (seedling), 44 (jointing stage), 62 (ten-leaf stage), and 75 (flowering stage) days after sowing in 2010. Values are the mean ± standard error of four replicates. Means with the same letter(s) are not significantly different between treatments at a specific growth stage ($P \leq 0.05$). N_BP_B: N and P broadcast; N_LP_L: localized N and P supply; D-N_LP_L: double (localized application at 0 and 55 days after sowing) localized N and P supply.

The root-length density at the depth of 0–15 cm was significantly greater in the N_LP_L and D-N_LP_L treatments than the N_BP_B treatment at 33 and 44 DAS (Fig. 4c, d).

Localized supply of ammonium plus P at 55 DAS (the second localized application in the D-N_LP_L treatment) also stimulated root proliferation in the soil patch where ammonium and P were applied at a depth of 10 cm from the soil surface along the mid-point line in the wide gap (Fig. 4e, f). The root-length density at the depth of 0–15 cm was significantly greater in the D-N_LP_L treatment than the N_LP_L and N_BP_B treatments at 75 DAS (20 d after the second localized application of ammonium plus 50% P), indicating an evident stimulation of root proliferation at the late growth stages. No difference in the root-length density was observed between the N_LP_L, D-N_LP_L, and N_BP_B treatments at the soil depth of 0–15 cm at 62 DAS (7 d after the second localized application of ammonium plus 50% P). There was no significant difference in the root-length density among the treatments at 15–30 and 30–45 cm depth.

Localized P and ammonium supply increased root proliferation in the soil nutrient patch (Fig. 5b), and the root length in the nutrient patch (narrow row in the N_LP_L treatment) was twice as much as that located just below the maize and about 13 times the plant roots grown at the wide gap in topsoil (0–15 cm). Therefore, at an early growth stage, most maize roots were concentrated in the nutrient-rich patch. In contrast, in the N_BP_B treatment, the root length in the narrow row was only 30% that located just below the maize and equal to the root length in topsoil (0–15 cm) of the wide row, as calculated from Fig. 5a.

DISCUSSION

Plants have the capacity to modify their root morphology in response to soil nutrient heterogeneity, and the root proliferation in nutrient patches is the most obvious response (Jackson *et al.*, 1990). Typical changes in root morphology include increased root length, biomass, and/or lateral root numbers (Drew, 1975; Robinson, 1994; Forde, 2002; Jing *et al.*, 2010).

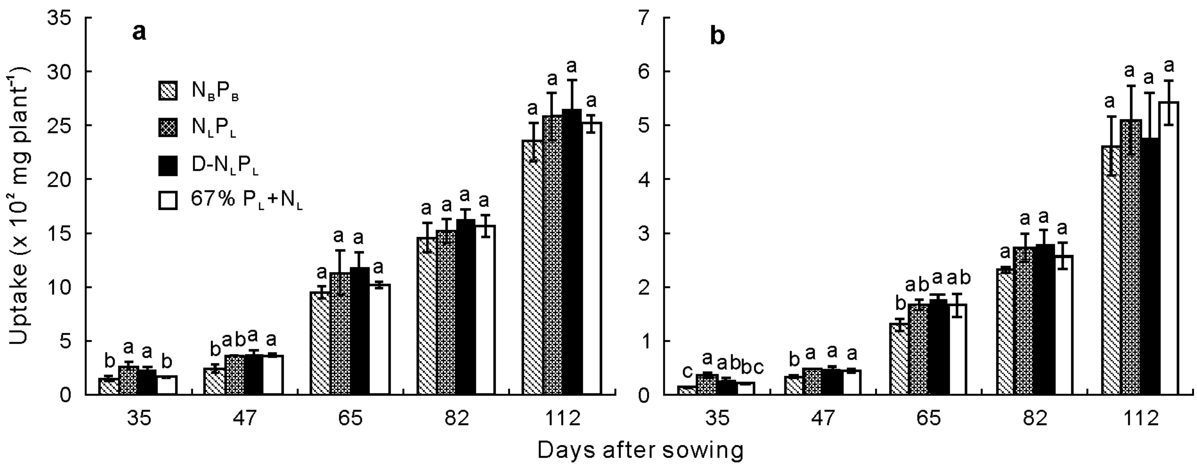

Fig. 3 Effects of different nutrient treatments on N (a) and P (a) accumulation by maize plants at 35 (seedling stage), 47 (jointing), 65 (ten-leaf stage), 82 (flowering stage), and 112 (grain-filling stage) days after sowing in 2009. Values are the mean ± standard error of four replicates. Means with the same letter(s) are not significantly different between treatments at a specific growth stage ($P \leq 0.05$). N_BP_B: N and P broadcast; N_LP_L: localized N and P supply; D-N_LP_L: double (localized application at 0 and 55 days after sowing) localized N and P supply; 67% P_L+N_L: localized 67% P and N supply.

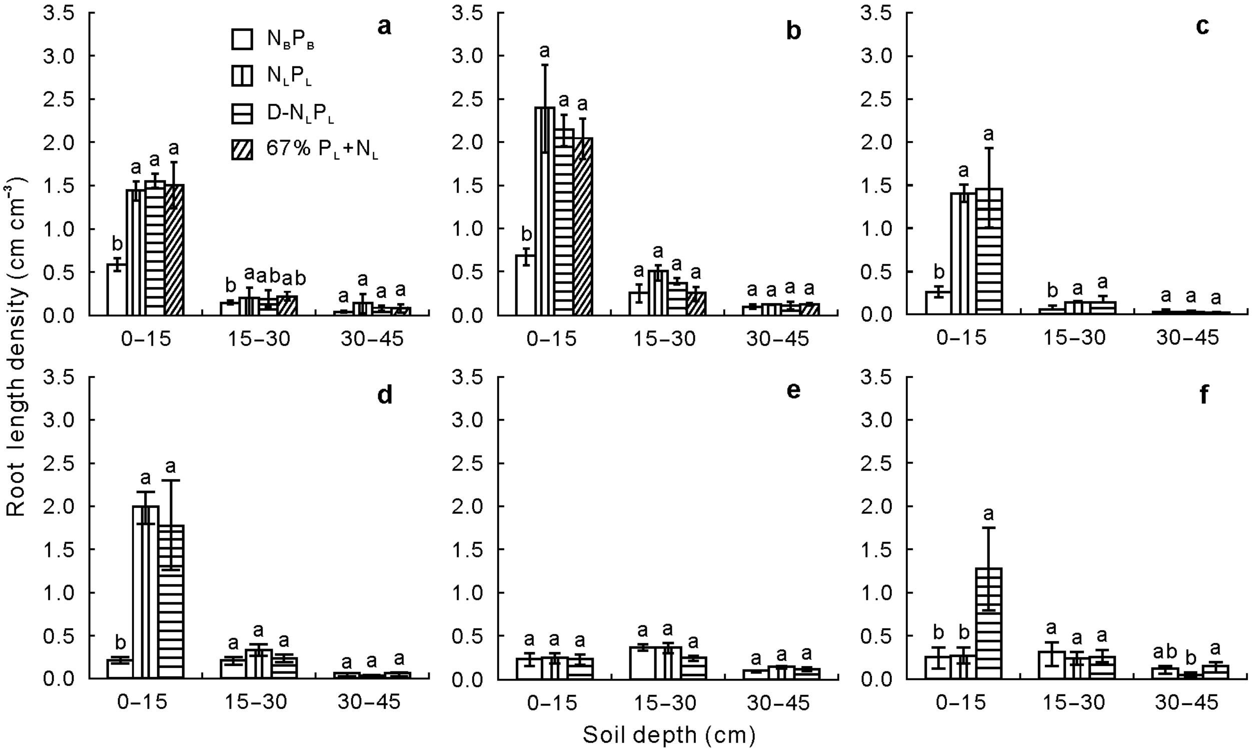

Fig. 4 Effects of different nutrient treatments on root length density measured in the middle of the narrow row at 35 (seedling stage) (a) and 47 (jointing stage) (b) days after sowing in 2009 and 33 (seedling stage) (c) and 44 (jointing stage) (d) days after sowing in 2010, and in the middle of the wide row at 62 (ten-leaf stage) (e) and 75 (flowering stage) (f) days after sowing in 2010. Value are the mean ± standard error of four replicates. Means with the same letter(s) are not significantly different between treatments at a given depth from soil surface ($P \leq 0.05$). N_BP_B: N and P broadcast; N_LP_L: localized N and P supply; D-N_LP_L: double (localized application at 0 and 55 days after sowing) localized N and P supply; 67% P_L+N_L: localized 67% P and N supply.

These changes are important for efficient nutrient acquisition and uptake by plants (Robinson, 1994, 2001). In the present study, localized P and ammonium supply induced proliferation of fine roots in the nutrient patch (Fig. 4), and most of these fine roots had a diameter of < 0.2 mm (Jing *et al.*, 2010), and thus had a high specific root length (SRL). The roots with high SRL have a more rapid rate of root proliferation than those with small SRL or thick roots (Eissenstat, 1991); the fine roots also show high nutrient-uptake efficiency in the patch (Gross *et al.*, 1993). These advantages led to increased shoot dry weight and nutrient uptake in the N_LP_L treatment at an early stage (Table III, Fig. 3), which is in agreement with the previous study (Jing *et al.*, 2010). The amount of P fertilizer applied can be substantially reduced when concentrated to the local site, strongly stimulating root proliferation and rhizosphere acidification (Jing *et al.*, 2010). Similarly, in an acidic soil, it is speculated that increased rhizosphere pH by locally applying nitrate plus P might help improve P availability and alleviate aluminum toxicity in the rhizosphere. However, the effects of localized application of P and ammonium (or nitrate depending on the soil pH) need to be further tested in different soil types. In the present study, the localized supply of 67% P and ammonium also enhanced root-length density without reduction in the shoot dry weight in comparison with the other treatments (Table I). It is suggested that localized P application with ammonium can significantly improve P accumulation as well as maize growth, especially at the early growth stages.

As predicted by the marginal value theorem (MVT), plants allocate more energy to a nutrient-rich patch than they do to a comparable volume in a homogeneous environment (McNickle and Cahill, 2009). Many researchers have reported that fine roots proliferate in a nutrient-rich patch. Root length density is a good indicator of spatial root distribution and the potential for soil resource exploitation and acquisition. In the present study, localized P and ammonium supply stimulated root proliferation in the soil nutrient patch (Fig. 5). At an early growth stage, most maize roots were concentrated in the nutrient-rich patch. The root proliferation was related to the heterogeneous nutrient distribution, and the similar phenomenon was observed in the previous study (Jing *et al.*, 2010).

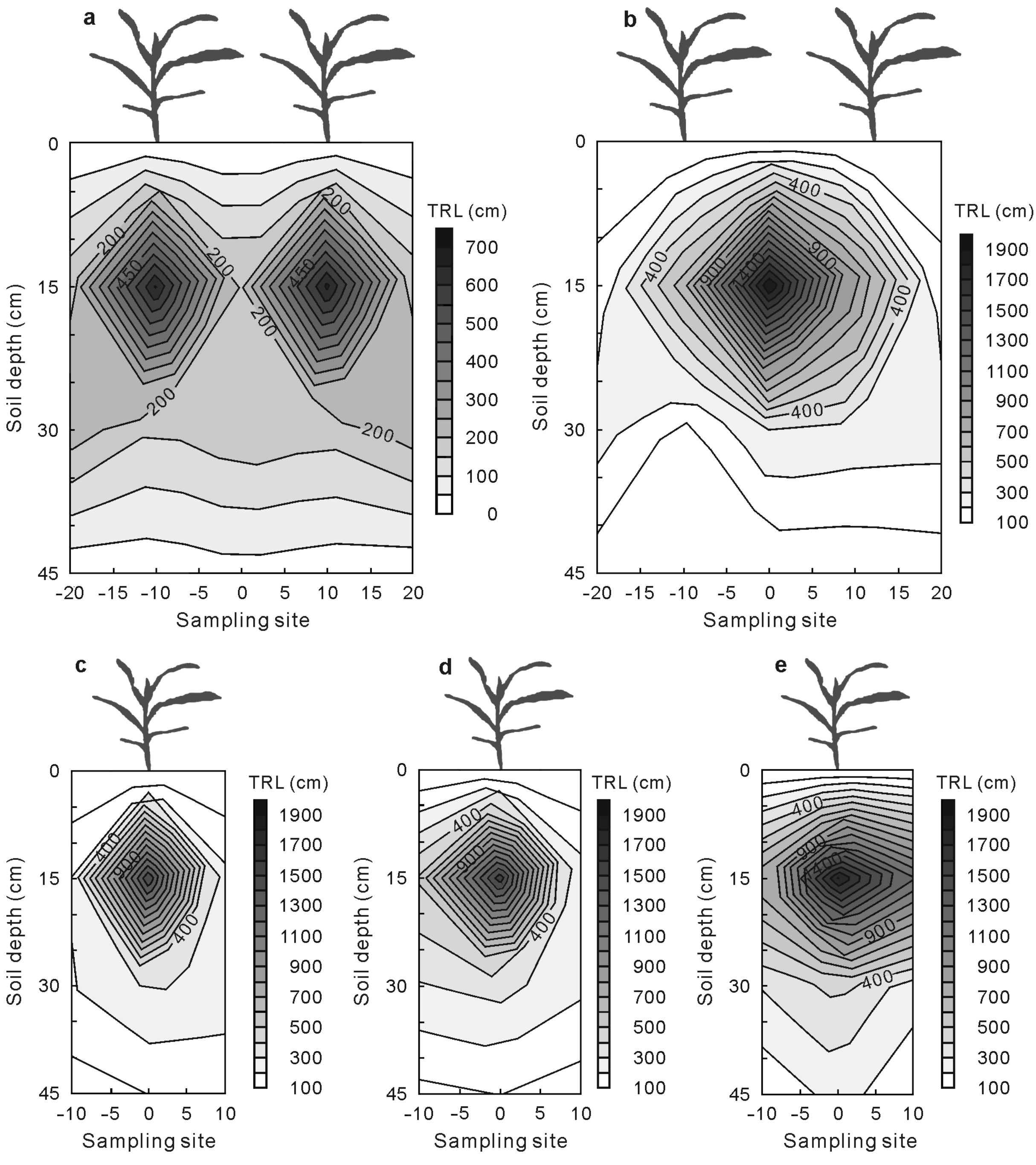

Fig. 5 Spatial distribution of total root length (TRL) of maize plants in response to localized nutrient supply in the field experiment in 2010: root distribution in the N_BP_B (a) and N_LP_L (b) treatments at 44 days after sowing (DAS); root distribution in the N_BP_B (c), N_LP_L (d), and D-N_LP_L (e) treatments at 75 DAS. The abscissa axis represents different sampling sites: 0 = the narrow row, −10 and 10 = the placement of plant growth, and −20 and 20 = wide row (a and b); or 0 = the placement of plant growth, −10 = narrow gap, and 10 = wide row (c, d, and e). The vertical coordinates represent the depth of soil: 0 = soil surface, 15 = 0–15 cm soil layer, 30 = 15–30 cm soil layer, and 45 = 30–45 cm soil layer. The total root length is indicated by the grayscale column on the right side of the figures, and the gradients of grayscale indicate different root lengths (in cm).

Fine roots in the soils with short-lived nutrient patches have a short life-span with high nutrient-uptake capacity, high maintenance respiration (Robinson, 1994; Eissenstat, 1991), and high root turnover rate (Gross *et al.*, 1993). The root life-span varies widely in different species. Some roots may live only a few weeks, and others one year or longer (Comas *et al.*, 2000; Bouma *et al.*, 2001; Tierney and Fahey, 2001; Wells and Eissenstat, 2001). In the present study, compared with the seedling stage (33 DAS), the fine root length of maize in the nutrient patch (narrow row in the N_LP_L treatment and wide row in the D-N_LP_L

treatment) at the flowering stage (75 DAS) decreased by 44%–62%, indicating a high death rate of roots in the patch, but there was no change in the soil homogeneously supplied with nutrients (narrow row in the N_BP_B treatment). As predicted by MVT, roots 'left' (or gave up) the patch when the nutrient concentration in the nutrient-rich patch decreased to a critical level. When the potential costs exceed the benefits, the root may not respond to the nutrient-rich patch (McNickle and Cahill, 2009). Considering the cost:benefit ratio and the root life-span, fine roots may be one of the most efficient ways to forage for and capture soil nutrients in a short time with maximal benefits and minimal costs, especially in competition with the neighbors.

In the natural environment, nutrient patches are variable in spatial and temporal distribution (Hodge, 2004). The intensity and timing of encountering a patch is also important; it was found that half-strength N-P-K patches induced the same root proliferation as the full-strength ones (Campbell and Grime, 1989; Hodge *et al.*, 1999). Hodge *et al.* (1999) reported that compared with the control, pulse supply of the same amount of nitrogen had no effects on the rate or total amount of N captured at the final harvest. In the present study, localized ammonium and half-intensity P (prior to the second application of 50% P in the D-N_LP_L treatment) also induced fine root proliferation similar to the N_LP_L treatment at an early stage (Fig. 4). Even with the localized nutrient supply at the later stage of maize growth (the second localized application of ammonium and 50% P in the wide row at 55 DAS in the D-N_LP_L treatment), the root length (Fig. 5e) was higher than those in the N_BP_B (Fig. 5c) and N_LP_L (Fig. 5d) treatments at 75 DAS. Compared with the N_BP_B and N_LP_L treatments, the late localized nutrient supply in the D-N_LP_L treatment did not increase the plant dry weight and nutrient capture (Table II, Fig. 3). Otherwise, at the early stage (44 DAS), the root length in the nutrient patches (wide row in the D-N_LP_L treatment) was only 70% of the root length that located just below the maize in the topsoil (Fig. 5e). So, the later localized ammonium plus P application stimulated the root but not shoot growth. Robinson (1994) pointed out that the root-to-shoot ratio usually increases or hardly changes in plants that have received localized nutrient supply, and the overall growth of plants is less affected by a heterogeneous nutrient supply than is seen in the changes in root system development. The present study also showed that the plasticity of roots existed throughout the plant growth cycle.

At an early stage of plant growth, plants invest large amounts of carbon into root development, and gain soil-based resources to meet their requirements. With the progression of plant growth and root development, the soil nutrients are becoming less limiting resources, and plants do not need to invest as much carbon into root development, directing them instead to shoots to increase capacity for capturing aboveground resources (such as light and space). The present study indicated that the contribution of root proliferation in nutrient-rich patches to nutrient uptake and maize growth was greater at the early than late growth stages. This may be related to decreased root proliferation in the nutrient patches (created by localized application of ammonium and P) at the late than early stages. The mechanisms behind the effect of localized application of P plus ammonium on root growth and nutrient uptake at different growth stages need further investigation.

CONCLUSIONS

Localized ammonium and P supply induced root proliferation and improved the nutrient-use efficiency at different growth stages of maize plants. The contribution to the plant growth of the root proliferation induced by the localized nutrient supply was dependent on the proportion of whole root length that was in the nutrient-rich patches. The increased nutrient uptake and plant growth at an early growth stage was related to the higher proportion of root length in the localized nutrient-enriched patch, but a relatively small effect on shoot growth at the later growth stages was attributed to a decreased proportion of root length in the nutrient patches. Fine roots may play a primary role in root foraging in nutrient patches. The functioning of root proliferation in the nutrient-rich patches needs to be elucidated.

REFERENCES

Bouma, T. J., Yanai, R. D., Elkin, A. D., Hartmond, U., Flores-Alva, D. E. and Eissenstat, D. M. 2001. Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. *New Phytol.* **150**: 685–695.

Campbell, B. D. and Grime, J. P. 1989. A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytol.* **112**: 261–267.

Campbell, B. D., Grime, J. P. and Mackey, J. M. L. 1991. A trade-off between scale and precision in resource foraging. *Oecologia.* **87**: 532–538.

Charnov, E. L. 1976. Optimal foraging: Attack strategy of a mantid. *Am. Nat.* **110**: 141–151.

Comas, L. H., Eissenstat, D. M. and Lakso, A. N. 2000. Assessing root death and root system dynamics in a study of grape canopy pruning. *New Phytol.* **147**: 171–178.

Drew, M. C. 1975. Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. *New Phytol.* **75**: 479–490.

McNickle, G. G. and Cahill, J. F. Jr. 2009. Plant root growth and the marginal value theorem. *PNAS.* **106**: 4747–4751.

Eissenstat, D. M. 1991. On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. *New Phytol.* **118**: 63–68.

Forde, B. G. 2002. Local and long-range signaling pathways regulating plant responses to nitrate. *Annu. Rev. Plant Biol.* **53**: 203–224.

Gleeson, S. K. and Fry, J. E. 1997. Root proliferation and marginal patch value. *Oikos.* **79**: 387–393.

Gross, K. L., Peters, A. and Pregitzer, K. S. 1993. Fine root growth and demographic responses to nutrient patches in four old-field plant species. *Oecologia.* **95**: 61–64.

Hodge, A., Stewart, J., Robinson, D., Griffiths, B. S. and Fitter, A. H. 1999. Plant, soil fauna and microbial responses to N-rich organic patches of contrasting temporal availability. *Soil Biol. Biochem.* **31**: 1517–1530.

Hodge, A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol.* **162**: 9–24.

Hodge, A. 2006. Plastic plants and patchy soils. *J. Exp. Bot.* **57**: 401–411.

Hutchings, M. J. and de Kroon, H. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* **25**: 159–238.

Jackson, R. B., Manwaring, J. H. and Caldwell, M. M. 1990. Rapid physiological adjustment of roots to localised soil enrichment. *Nature.* **344**: 58–59.

Jing, J., Rui, Y. , Zhang, F., Rengel, Z. and Shen, J. 2010. Localized application of phosphorus and ammonium improves growth of maize seedlings by stimulating root proliferation and rhizosphere acidification. *Field Crop Res.* **119**: 355–364.

Nonacs, P. 2001. State dependent behavior and the marginal value theorem. *Behav. Ecol.* **12**: 71–83.

Reich, P. B., Walters, M. B., Tjoelker, M. G., Vanderklein, D. and Buschena, C. 1998. Photosythesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Funct. Ecol.* **12**: 395–405.

Robinson, D. 1994. The response of plants to non-uniform supplies of nutrients. *New Phytol.* **127**: 635–674.

Robinson, D. 2001. Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil. *Plant Soil.* **232**: 41–50.

Sanderson, J. B., Daynard, T. B. and Tollenaar, M. 1981. A mathematical model of the shape of corn leaves. *Can. J. Plant Sci.* **61**: 1009–1011.

Tjoelker, M. G., Craine, J. M., Wedin, D., Reich, P. B. and Tilman, D. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol.* **167**: 493–508.

Tierney, G. L. and Fahey, T. J. 2001. Evaluating minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest. *Plant Soil.* **229**: 167–176.

Weligama, C., Tang, C., Sale, P. W. G., Conyers, M. K. and Liu, D. L. 2008. Localised nitrate and phosphate application enhances root proliferation by wheat and maximises rhizosphere alkalisation in acid subsoil. *Plant Soil.* **312**: 101–115.

Wells, C. E. and Eissenstat, D. M. 2001. Marked differences in survivorship among apple roots of different diameters. *Ecology.* **82**: 882–892.

Zhang, H., Jennings, A., Barlow, P. W. and Forde, B. G. 1999. Dual pathways for regulation of root branching by nitrate. *PNAS.* **96**: 6529–6534.