Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China

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Abstract

Root and rhizosphere research has been conducted for many decades, but the underlying strategy of root/rhizosphere processes and management in intensive cropping systems remain largely to be determined. Improved grain production to meet the food demand of an increasing population has been highly dependent on chemical fertilizer input based on the traditionally assumed notion of 'high input, high output', which results in overuse of fertilizers but ignores the biological potential of roots or rhizosphere for efficient mobilization and acquisition of soil nutrients. Root exploration in soil nutrient resources and root-induced rhizosphere processes plays an important role in controlling nutrient transformation, efficient nutrient acquisition and use, and thus crop productivity. The efficiency of root/rhizosphere in terms of improved nutrient mobilization, acquisition, and use can be fully exploited by: (1) manipulating root growth (i.e. root development and size, root system architecture, and distribution); (2) regulating rhizosphere processes (i.e. rhizosphere acidification, organic anion and acid phosphatase exudation, localized application of nutrients, rhizosphere interactions, and use of efficient crop genotypes); and (3) optimizing root zone management to synchronize root growth and soil nutrient supply with demand of nutrients in cropping systems. Experiments have shown that root/rhizosphere management is an effective approach to increase both nutrient use efficiency and crop productivity for sustainable crop production. The objectives of this paper are to summarize the principles of root/rhizosphere management and provide an overview of some successful case studies on how to exploit the biological potential of root system and rhizosphere processes to improve crop productivity and nutrient use efficiency.

Key words: Crop productivity, intensive agriculture, nutrient use efficiency, rhizosphere management, rhizosphere processes, root growth.

Principle of root/rhizosphere management

‘Using less produces more’ is becoming a promising characteristic for sustainability of modern agriculture despite the great contribution of intensive agriculture with ‘high input, high output’ to the growth of food production in the past. The status of agriculture today is more complex than before because of the increased demand for global food production while also protecting environmental quality and conserving natural resources in the coming decades. Simultaneously achieving high nutrient use efficiency and high crop productivity has become a challenge with increased global demand for food, depletion of natural resources, and deterioration of environmental conditions (Cassman, 1999; Tilman et al., 2002; Cassman et al., 2003). For example, in the past half century, Chinese cereal grain yields increased 3.5-fold from 1.2 to 5.4 t ha$^{-1}$; however, cereal grain yields increased by only 65% from 1980 to 2010, while the consumption of chemical...
fertilizers increased by 512% (Zhang et al., 2011, 2012). Total crop yield in intensive Chinese farming systems has failed to increase in proportion by increasing the inputs of chemical fertilizers over the last 20 years, leading to low nutrient use efficiency and increasing environmental problems. This is mainly attributed to the overuse of chemical fertilizers while ignoring the intrinsic potential benefits of biological processes in crop exploitation of nutrient resources in the soil.

Soil nutrients are taken up by plant roots via the rhizosphere, which is the key zone of interaction between plants and soils. Therefore, root growth and rhizosphere processes have a great influence on soil nutrient transformation, mobilization, and efficient use by plants. Plant roots can not only highly regulate morphological traits to adapt to soil environmental conditions, but also significantly modify rhizosphere processes through their physiological activities, particularly the exudation of organic acids, phosphatases, and some signalling substances, proton release, and redox changes (Hinsinger, 2001; Hinsinger et al., 2009; Zhang et al., 2010; Marschner, 2012). The root-induced rhizosphere processes not only determine mobilization and acquisition of soil nutrients as well as microbial dynamics, but also control nutrient use efficiency by crops, and thus profoundly influence crop production and sustainability (Zhang et al., 2010). Therefore, manipulating root growth and rhizosphere processes provides an effective approach to improve nutrient use efficiency and crop productivity simultaneously.

Root/rhizosphere management strategies lay emphasis on maximizing the efficiency of root and rhizosphere processes in nutrient mobilization, acquisition, and use by crops rather than depending solely on excessive application of chemical fertilizers in intensive farming systems. The efficiency of root and rhizosphere processes is highly dependent on inherent soil fertility and the status of soil nutrient supply, which is controlled by the input of external nutrients. It is well known that root growth and expansion can be greatly constrained when the available soil nutrient supply is extremely low. The efficiency of root and rhizosphere processes can be enhanced with increasing intensity of soil nutrient supply. However, overuse of fertilizers may lead to high concentrations of nutrients in the rhizosphere, resulting in inhibition of root growth and rhizosphere processes (Li et al., 2008; Mi et al., 2010; Zhang et al., 2010). Synchronizing root-zone nutrient supply with crop demands spatially and temporally at an optimal level of nutrient supply in the rhizosphere is important for maximizing the efficiency of the root/rhizosphere in nutrient mobilization and acquisition (Figs. 1 and 2). The main strategies of root/rhizosphere management are: (1) manipulating root growth in terms of both morphological and physiological traits; (2) intensifying rhizosphere processes in terms of acidification and carboxylate exudation; and (3) synchronizing root-zone nutrient supply with crop demand by integrated soil–crop system management (Zhang et al., 2010; Chen et al., 2011). Root/rhizosphere management has been demonstrated to be an effective approach to simultaneously enhance nutrient use efficiency and crop yields for sustainable crop production in Chinese intensive agriculture.
Maximizing root efficiency

Root efficiency in response to nutrient supply

There is evidence indicating that plants exhibit large differences in their capacity to use soil nutrients through modifying root growth and root exudation. We found that root morphological development was greatly inhibited when excessive nitrogen (N) was supplied during intensive maize (Zea mays L.) production (Fig. 3). In principle, N deficiency increases root growth, resulting in longer axial roots (primary roots, seminal roots, and nodal roots) and this helps maize roots to explore a larger soil volume and thus increases the spatial N availability (Tian et al., 2008; Marschner, 2012); however, long-term N deficiency stunts root growth due to insufficient N (Wang et al., 2003). But also, root elongation can be inhibited if the N supply is too high. In maize, for example, root length was found to be reduced when the nitrate concentration in culture solutions was more than 5 mmol l⁻¹ (Tian et al., 2008). Only at the level of N supply was there optimal development of the root system, resulting in increased nutrient use efficiency. There was optimum lateral root growth when the nitrate supply was maintained at around 1 mmol l⁻¹ in agar gel-based culture for maize (Guo et al., 2005). Roots in the field are exposed to changing N levels for a longer time, and therefore their responses to N supplies may differ from that found in solution culture systems where the growth period is relatively short. For example, Morell et al. (2011) found that grain yield but not root growth in barley was affected by N fertilization in field conditions. In maize, there are conflicting results concerning whether N application causes increase (Maizlish et al., 1980) or decrease (Eghball and Maranville, 1993) in root growth. Nevertheless, in a 2-year experiment across three types of soils, a moderate but significant correlation was found between soil nitrate concentration and maize root length at silking stage (Fig. 3). Similar responses were found in the roots of Arabidopsis seedlings growing on agar plates uniformly supplied with a range of KNO₃ concentrations (0.01–50 mmol l⁻¹, Zhang and Forde, 1998; Zhang et al., 1999). The results reveal that high rates of nitrate supply have no effect on lateral root initiation but cause a pronounced delay in lateral root development at around the time of emergence from the parent root and thus result in 100% growth inhibition of the lateral roots by 50 mmol l⁻¹ KNO₃ (a concentration higher than would normally be found in the soil, Forde and Lorenzo, 2001). Therefore, root growth can be manipulated or optimized via optimizing soil N status in the root zone or rhizosphere.

Under field conditions, nitrate that moves down to deeper soil layers by heavy rainfall is not spatially available if plant roots cannot grow deep enough. Modelling work has concluded that root system architecture, with a larger investment in fine roots deep in the soil, will increase crop yields by accessing extra soil resources from the whole soil profile (King et al., 2003). Research comparing different maize genotypes suggests that root length density deep in the soil (30–150 cm)
has a significant positive correlation with nitrate depletion (Wiesler and Horst, 1994). Therefore, increasing root proliferation in deep soil by crop improvement through breeding (Mi et al., 2010; Lynch, 2007, 2011) or agronomic N management may be a promising way of enhancing N use efficiency under high N input conditions. Our experiment demonstrates that the vertical distribution of roots in the soil profile can be manipulated through N management to enhance nutrient capture and uptake by crops (Mi et al., 2010; Zhang et al., 2012).

In intensive cropping systems characterized by high input and high output, chemical fertilizers are usually overused. However, overapplication of N cannot further increase grain yields in most cases. Plant N content is significantly correlated with shoot biomass (Reich et al., 2006). Under the same conditions, an N-efficient maize variety has higher shoot biomass and larger root size and takes up more N than does an N-inefficient variety (Kamprath et al., 1982; Peng et al., 2010). There is a positive relationship between grain yield and root size in maize (Barber and Mackay, 1986). Maize cultivars having high root length density enhanced the utilization of soil N and thus reduced the risk of nitrate leaching (Wiesler and Horst, 1994). However, in some cases with high soil fertility, the amount of N taken up by maize can be driven by the demand of shoot growth rather than by the size of the root system (Peng et al., 2010; Ning et al., 2012). In general, increasing application of N fertilizer will increase grain yield. However, this does not mean that the more N that is applied the higher the grain yield that can be achieved. A linear relationship between shoot N content and green leaf area has been reported for a wide range of crops (Lemaire and Gastal, 1997; Plénet and Lemaire, 1999; Lemaire et al., 2007). There is a critical N concentration, e.g. the minimum percentage of N in shoots required to produce the maximum aerial biomass at a given time (Plénet and Lemaire, 1999). Overapplication of N cannot further increase shoot biomass and grain yield of maize plants (Boomsma et al., 2009). Under field conditions, our results demonstrate that in comparison with the optimized N application, conventional N supply (over-application) inhibits root growth at both the early growth stage (Fig. 4A) and the rapid growing stage (Fig. 4B), and cannot increase the final N content of the whole plant and thus the final grain yield (Fig. 4C and D). On the other hand, optimized N application involves not only controlling the total amount of chemical N fertilizer, but also synchronizing crop N demand and soil N supply by splitting the N applications (Peng et al., 2012). In addition,

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**Fig. 4.** Comparison of root growth in response to different N rates at the early stage of growth (A) and the whole growth period (B) and changes in grain yield (C) and total plant N content (D) at maturity with conventional and optimized N regimes in the field. Bars represent the standard error of the mean (n = 4).
optimized N supply delayed root mortality at harvest, especially in the top 30 cm soil layer, compared with the conventional N supply. Thus, optimized N application can not only improve N use efficiency, but also reduce the risk of N leaching and potential environmental pollution (Ju et al., 2009; Vitousek et al., 2009; Mi et al., 2010; Zhang et al., 2012).

Root proliferation in response to localized nutrient supply

The capacity to better match root systems to the soil nutrient supply offers the potential to optimize nutrient use efficiency and crop productivity. The ideal root architecture for maize in our study is characterized by high sensitivity of enhanced root growth to both homogenous nutrient supply and localized nutrient patches (Mi et al., 2010). Root proliferation can be enhanced in heterogeneous nutrient-rich patches for efficient exploitation of soil nutrient resources. Many crop species exhibit the stimulating responses to localized nutrient supply, including maize (Jing et al., 2010, 2012; Liu et al., 2010), white lupin (Lupinus albus, Li et al., 2010), barley (Hordeum vulgare, Drew, 1975), and wheat (Triticum vulgare, Yao and Barber, 1986). Localized nitrate supply significantly increased maize lateral root growth (Liu et al., 2010). Local applications of nitrate reduced shoot-to-root auxin transport and reduced auxin concentration in roots to a level more suitable for lateral-root growth (Liu et al., 2010, Mi et al., 2010). Cluster roots can be greatly induced by P deficiency for the whole root system in white lupin (Neumann et al., 1999; Shen et al., 2003; Vance et al., 2003; Lambers et al., 2006), but the distribution of cluster roots can be shifted from the P-deficient root zone to P-rich or organic matter-rich patches to increase the intensity of soil foraging (Shen et al., 2005; Li et al., 2010). The localized applications of N and P fertilizers have been recommended for many decades in China. Phosphorus (P) banding near the root zone is recommended over conventional broadcast applications because banding fertilization saturates the soil with P in a relatively small area within the root zone, increasing P availability and stimulating root proliferation. Applying P with or near the seeds or starter-band N and P fertilizers at early growth stages is recognized to be an effective strategy for stimulating root development and establishment of a virtually ideal root architecture and increasing yields, particularly in the early spring season at low temperatures.

Localized supply of P plus ammonium significantly increased chlorophyll content and leaf area, leading to increased biomass of shoots at early growth stages (Jing et al., 2010). This practice increased leaf expansion rate by 20–50%, total root length by 23–30%, and plant growth rate by 18–77% at early growth stages in comparison with the conventional broadcast treatments. The root-length density at a depth of 0–15 cm was greater in treatments with localized application of P plus ammonium, with a greater proportion of fine roots (diameter <0.2 mm). Localized supply of P plus ammonium markedly modified root growth and rhizosphere processes by stimulating root proliferation and thus significantly increasing the acquisition of N and P by plants (Jing et al., 2010). The results indicate that localized application of P combined with ammonium addition significantly increased maize growth and acquisition of N and P at the early growth stages by stimulating root proliferation (Fig. 5). Further study has shown that localized fertilization with P plus N elicits an ammonium-dependent enhancement of maize root growth and nutrient uptake at the seedling stage in a calcareous soil (Jing et al., 2012). These results suggest that positioning and manipulating root growth and distribution in the field may be an effective management strategy for improving nutrient use efficiency and crop growth.

Ideotype root system architecture

Plants show high plasticity in root growth and development in response to varied environmental conditions (Hodge, 2006; Lynch 2011). Root response can be induced by nutrient supply intensity on the whole as well as spatiotemporal resource variation, especially the availability of water and nutrients (de Kroon et al., 2005; Hodge, 2006). Based on the above analysis, root size can be determined by soil nutrient concentrations whereas root distribution and proliferation are highly dependent on the localized supply of nutrients in the soil. It is suggested that an ideotype root architecture for efficient N acquisition by maize should include: (i) deeper roots with high activity that are able to adsorb soil nitrate before it moves downward into deep soil with consequent by leaching; and (ii) strong response of lateral root growth to localized N supply so as to utilize unevenly distributed nitrate especially under limited N conditions (Fig. 6, Mi et al., 2010). It was reported that more aerenchyma tissues in the cortex of the roots can also be an important trait that contributes to efficient N uptake with lower carbon input in root growth (Postma and Lynch, 2011). Thus, a deeper root with more aerenchyma tissues is important for efficient capture of soil resources. This root architecture may also be efficient in the uptake of deep water and therefore help to increase drought resistance (Hund et al., 2009). However, since the higher phosphorus availability was found in surface soil strata, a shallow root system with enhanced adventitious roots is relatively important for crops to absorb phosphorus (Lynch, 2007, 2011). Therefore, an efficient maize genotype with the ideotype root architecture should be able to effectively integrate different root functions in terms of capture and use of various soil resources, especially soil N, P, and water, both spatially and temporally (Fig. 6).

Maximizing rhizosphere efficiency

Rhizosphere processes reflect dynamic changes in rhizosphere biology and chemistry for the interactions between plants and soils and are bottlenecks controlling nutrient transformation, availability, and efficient use by plants. A better manipulation of rhizosphere processes may provide an effective approach for improving nutrient use efficiency and crop productivity simultaneously through exploiting biological potential for efficient acquisition and utilization of nutrients and reducing
overreliance on the application of chemical fertilizers. The rhizosphere efficiency can be enhanced through optimizing nutrient supply. The rhizosphere efficiency, to some extent, can be repressed by either severe nutrient deficiency or excessive nutrient supply (Fig. 1, Zhang et al., 2010). This approach can modify rhizosphere processes and efficiency by regulating root development and thus carboxylate exudation, proton release, and acid phosphatase activity in the interface between roots and the soil.

Rhizosphere processes in response to uniform nutrient supply

It is well known that root exudation can profoundly affect soil nutrient mobilization and acquisition through altering rhizosphere chemical and biological processes (Neumann et al., 1999; Lambers et al., 2006; Zhang et al., 2010). Plant roots can explore soil nutrients within broad concentration ranges of the nutrients. The varied nutrient concentrations in soil have an evident influence on plant nutritional status and thus produce a feedback from aboveground to belowground to modify the rhizosphere environment (Zhang et al., 2010). Our study shows that citrate exudation by white lupin roots is highly controlled by plant P status and that the proportion of cluster roots and the rate of citrate exudation decreases sharply with increasing P concentration in the shoots up to a critical level of 2 mg P (g dryweight)\(^{-1}\) (Li et al., 2008). When the shoot P concentration was above 2 mg (g dryweight)\(^{-1}\), citrate exudation from the roots decreased by 74% compared with a shoot P concentration of 1 mg (g dryweight)\(^{-1}\). The results indicate that citrate exudation can be inhibited by increased shoot P nutrition in association with external P application. Excessive nutrient input through fertilization may cause a high concentration of nutrients in the rhizosphere, resulting in the inhibition of root growth and rhizosphere efficiency in the efficient mobilization and use of soil nutrients, especially for P (Shen et al., 2011). Our field trials in intensive farming systems show that excessive nutrient input enhances the available nutrient concentration in the root zone, which greatly inhibits potential P mobilization and uptake (i.e. decreased expression of genes mediating P mobilization and uptake processes). Optimizing P-efficient gene

Fig. 5. Maize seedling growth as affected by localized application of phosphate with addition of ammonium as the treatment of root/rhizosphere management (RM) in comparison with broadcasting control representing conventional fertilization (A) and by rhizosphere acidification at RM (yellow) (B), and root proliferation (C) in the localized nutrient patch of maize. (Plate B, reprinted from Field Crops Research 119, Jing JY, Rui YK, Zhang FS, Rengel Z, Shen JB. Localized application of phosphorus and ammonium improves growth of maize seedlings by stimulating root proliferation and rhizosphere acidification, 355–364, Copyright (2010), with permission from Elsevier.)
expression by regulating nutrient supply intensity to a proper level may be important to enhance P use efficiency through exploring efficient biological potential. These small changes in rhizosphere processes may lead to large effects on rhizosphere efficiency, resulting in increased nutrient use efficiency and crop growth.

**Rhizosphere processes in response to localized application of nutrients**

It is clear that nutrients have profound effects on many aspects of root development and thus concomitant rhizosphere processes. Plant roots have high plasticity to soil environmental changes and can sense and respond to heterogeneous nutrient patches in the soil profile (Robinson, 1994; Hodge, 2006; Jing et al., 2010). Most mineral nutrients were taken up by plants through the rhizosphere where root exudates play a dominant role in driving interactions among plant roots, soil and microorganisms. Plant root exudates consist of a complex mixture of organic acid anions, phytosiderophores, sugars, amino acids, and enzymes (i.e. acid phosphatases and phytase), which have major direct or indirect effects on the acquisition of mineral nutrients required for plant growth (Dakora and Phillips, 2002). In a split-root experiment with white lupin, the exudation rates of protons, citrate, and acid phosphatase in both root halves increased significantly when both halves of the root system were exposed to P-deficient treatments (Shen et al., 2005). Localized P supply to half the roots significantly increased the shoot P concentration and decreased the exudation rate of citrate and acid phosphatase, but the exudation rate of citrate in the P-deprived root half was higher than that of the P-supplied treatment to both root halves. Localized P supply also reduced proton release. The results indicate that citrate exudation was predominantly regulated by shoot P status and also affected by the localized supply of external P and that proton release was inhibited by the localized P supply by altering the balance of anion and cation uptake (Shen et al., 2003, 2005; Li et al., 2008, 2010; Marschner, 2012). Citrate exudation from white lupin was thought to be highly dependent on root zone, developmental stage, P nutritional status, and aluminium stress (Wang et al., 2007). This provides a basis for understanding the relationship between citrate exudation and the adaptation of white lupin to acidic soils with low P fertility and with aluminium toxicity. This analysis suggests that rhizosphere processes in terms of carboxylate exudation, proton release, and acid phosphatases can be, at least to some extent, manipulated through altering nutrient supply and composition or other environmental stresses.

**Rhizosphere acidification can enhance P mobilization and acquisition from soil by plants** (Hinsinger, 2001; Hinsinger et al., 2009; Zhang et al., 2010). The form of N supply, to a great extent, controls the uptake ratio of cations and anions and thus influences root apoplastic pH and rhizosphere pH (Raven, 1985; Marschner, 2012). Ammonium supply can induce release of protons from roots and thus...
cause rhizosphere acidification but nitrate supply can induce hydroxyl secretion by roots and thus cause rhizosphere alkalinization (Marschner, 2012). Our studies show that localized application of ammonium combined with superphosphate significantly increases crop growth in a calcareous soil because ammonium uptake promotes proton release by roots and thus decreases rhizosphere pH, leading to increased bioavailability of phosphates (Jing et al., 2010, 2012, Fig. 5). Furthermore, localized supply of ammonium plus superphosphate also markedly stimulates root proliferation, especially of fine roots. The results indicate that localized application of P combined with ammonium addition can significantly enhance maize growth and acquisition of N and P in the early growth stages not only by stimulating root proliferation but also by rhizosphere acidification. Duncan and Ohlrogge (1959) and Miller and Ohlrogge (1958) found that N and P banded together increased P absorption due to extensive proliferation of roots in the fertilized zone. Phosphorus supply combined with ammonium (as opposed to nitrate) could increase P accumulation, with increased root proliferation (Jing et al., 2010) and enhanced P uptake rates (Hoffmann et al., 1994). The magnitude of root proliferation and rhizosphere processes in the localized nutrient-rich patches was highly dependent on the specific nutrient composition and their interaction. We suggest that modifying rhizosphere processes by changing the intensity and composition of the localized nutrient supply in the field may be an effective management strategy for increasing nutrient use efficiency and plant growth. In our intensive farming system in north China, rhizosphere management not only increases maize yield by 5–15% with high yields of 12–15 t ha⁻¹, but also saves considerable chemical inputs by reducing fertilizer application (by 40–50% for fertilizer N and by 33% for superphosphates, Zhang et al., 2010).

Rhizosphere acidification that benefits sparingly available nutrient mobilization can also be strengthened by employing suitable fractions of fertilizer nutrients as well as efficient crop genotypes that can acidify their rhizosphere (Fig. 5). For example, application of monoammonium phosphate and ammonium sulphate may result in lower pH in the fertilizer microsites in comparison to diammonium phosphate, which is in favour of nutrient mobilization and capture by roots, especially in calcareous soils. Adopting efficient crop species or genotypes that can acidify the rhizosphere and mobilize insoluble nutrients in soils is an effective approach to increase P availability in lupin, faba bean (Vicia faba L.), soybean (Glycine max), chickpea (Cicer arietinum), common bean (Phaseolus vulgaris), and alfalfa (Medicago sativa). Moreover, the rhizosphere processes can also be engineered by genetic modification of crops and microbial biological activities (Ryan et al., 2009). In intensive agriculture, our studies indicate that overuse of chemical fertilizer N may promote soil acidification in the long term (Guo et al., 2010). Therefore, it is important to reduce chemical fertilizer inputs and use localized N and P fertilizers as starters to stimulate root growth and intensify rhizosphere processes for improving nutrient acquisition and crop production.

### Rhizosphere interactions between intercropped legumes and cereals

Advantages of intercropping have been demonstrated in numerous cropping systems in China and this has been used as one of the most important strategies for increasing crop yields in irrigated areas in northwest China. Legume/cereal intercrops are known to yield more because of legume N₂ fixation. However, in a P-deficient intercropping system, P can be mobilized by legume species because legume crops can acidify the rhizosphere through proton release in association with P deficiency and N fixation (Li et al., 2007, 2010). Phosphorus mobilized by roots of faba bean may increase the growth of the intercropped maize, resulting in significant yield increases on P-deficient soils. The results from 4-year field experiments show that maize yield increased by 43% and faba bean by 26% (Li et al., 2007). Such over-yielding of maize was related to rhizosphere interactions between faba bean and maize because faba bean acidified its rhizosphere, with pH declining up to 2 units under agro cultural conditions, but maize exerted the opposite effect on its rhizosphere. The effect of rhizosphere acidification of faba bean on maize may cause a P-nutrition improvement in faba bean/maize intercropping through interspecific rhizosphere interactions between faba bean and maize because a decrease in the soil pH from 6.5 to 4.1 can result in at least a 10-fold increase in the P released into soil solution (Gristed et al., 1982). Moreover, both malate and citrate concentrations in the rhizosphere soil of faba bean were greater than those in maize. Other work has shown that piscidic acid exuded from the roots of pigeon pea promoted the release of P from FePO₄ by chelating iron (Ae et al., 1990). Citric and malic acids are the major components of root exudates of lupine and play an important role in P uptake in a P-deficient soil (Neumann et al., 1999; Dakora and Phillips, 2002; Lambers et al., 2006). Under organic P supply, chickpea has been found to improve P nutrition of wheat because of increased acid phosphatase activity in the rhizosphere besides rhizosphere acidification (Li et al., 2004). These studies have shown that a plant releasing great amounts of protons, organic acids, or phosphatase mobilizes inorganic P or organic P in soil, which benefits the plant itself and other plant species whose roots are strongly intermingled in intercropping systems (Li et al., 2007).

In legume and cereal intercropping systems, our studies have shown facilitation in terms of N and P utilization, which results mainly from rhizosphere interactions induced by the root systems of both crop species, and the rhizosphere interactions might be further intensified through strong intermingling of their root systems. Besides facilitation, competition and complementarity in terms of resource use between two intercropped species also play an important role in the yield-increasing advantages of intercropping systems (Zhang et al., 2010). No doubt the wide use of intercropping in traditional Chinese farming systems contributed more to ensure grain production for an increasing population. However, the underlying mechanisms in rhizosphere interactions in favour of facilitating N and P utilization remain largely to be determined (Zhang et al., 2010; Shen et al., 2011) despite some
progress in examining relationships between rhizosphere processes and changes in P availability (Wang et al., 2007; Li et al., 2008). Since rhizosphere interactions vary greatly with soil type and plant species (Hinsinger, 2001; Hinsinger et al., 2009), it is suggested that optimizing crop combination and nutrient management in intercropping systems through better understanding of rhizosphere interactions provides an effective approach to improve sustainable crop production with high yield, high nutrient use efficiency, and friendly environment in China (Zhang et al., 2010, 2012).

**Up-scaling root-zone management in cropping systems**

In cropping systems, the rhizospheres can overlay each other and form a huge continuum with development of root systems in the whole root zone, where root/rhizosphere interactions occur among plants, soils, and microorganisms and even between different plant species in intercropping systems (Zhang et al., 2010; Shen et al., 2011). Crop yield can be increased through optimizing fertilizer application by controlling the nutrient supply in the root zone at an optimal level, resulting in maximizing the biological potential of crops, matching high-yielding crop nutrient requirements and reducing nutrient losses in environments (Fig. 2, Zhang et al., 2010; Shen et al., 2011; Zhang et al., 2012). Nutrient supply and crop requirements in high-yielding crop systems must be matched in quantity and synchronized spatially and temporally, and the biological potential of the root system must also be taken into consideration. Nutrient application can be effectively controlled by restricting the total chemical fertilizer application rate based on nutrient balance and matching crop requirements by reasonably splitting fertilization at different growth stages. For example, N fertilizer can be reduced from 588 to 286 kg N ha⁻¹ year⁻¹ without a loss in yield, but with decreased N losses by 50% (Ju et al., 2009).

As for an in-season root-zone nutrient management strategy, soil nutrient supply in the root zone is controlled within a reasonable range that matches the quantity required by the crop, is synchronized in terms of time and crop growth, and is coupled in space to nutrient supply and crop nutrient requirements, especially in N management (Cui et al., 2008). Maize crop growth and N requirement are relatively low during the early growth stages. Overapplication of N fertilizer during this period increases the risk of nitrate leaching and results in excessive crop growth susceptible to disease and lodging. Therefore, N fertilizer (around 60–70% of the total N fertilizer input) should be applied mainly during the rapid growth stages of crops to achieve synchronization between the N supply and crop demand. Root-zone nutrient management can fully exploit root/rhizosphere efficiency in efficient soil nutrient acquisition from the root zone by plants while minimizing chemical fertilizer application, which may profoundly affect crop growth. Vigorous shoot growth can further stimulate root growth and activity through a positive feedback from aboveground to belowground (Zhang et al., 2010). Based on this analysis, we developed an integrated soil–crop system management approach, designed to achieve maximum use of various resources from aboveground (solar radiation and temperature) and belowground (nutrient supply with depth of root zone) and greater synchrony between crop demand for N and its supply from soil, environment, and applied inputs (Chen et al., 2011). By adopting this approach, the fertilizer N efficiency (represented as yield per unit fertilizer N applied, kg kg⁻¹) increased from 26 to 57 kg kg⁻¹, with a significant increase in grain yield from 6.8 to 13 t ha⁻¹ despite a decrease of 7.8% in N input from fertilizer and manure (from 257 to 237 kg N ha⁻¹, Chen et al., 2011). The results of 66 on-farm experimental plots have shown that integrated soil–crop system management is an effective approach for increasing crop productivity and nutrient use efficiency, which represents an important case for implementation of sustainable intensification of modern agriculture. Taken together, development and application of root/rhizosphere management in intensive agriculture of China may provide important lessons (negative effect of overfertilization in Chinese intensive agriculture with high input and high output, but low nutrient use efficiency and high environment risk) and experience (exploring root/rhizosphere biology to simultaneously improve crop productivity and resource use efficiency with reduced chemical fertilizer application) for the world, especially in rapidly growing economies for ensuring food security.

**Conclusions**

Our studies indicate that root/rhizosphere management provides a unique opportunity to realize high nutrient use efficiency, high crop productivity, and environmental protection simultaneously, which is a major challenge faced by Chinese intensive agriculture. Root/rhizosphere management involves manipulating root growth, rhizosphere modification, localized nutrient application, rhizosphere interactions in intercropping, and the use of efficient crop genotypes with an aim to exploit the biological potential for efficient nutrient acquisition by plant roots rather than overuse of chemical fertilizers (Fig. 7). Fertilizers are used not only to provide mineral nutrition for crops but more importantly to act as regulators of root growth or rhizosphere processes. The nutrient inputs in intensive farming systems should be optimized to achieve both high crop productivity and high nutrient use efficiency through maximizing root/rhizosphere efficiency in nutrient mobilization and acquisition. The strategies of root/rhizosphere management reflect a shift from conventional nutrient management to regulating root morphology and managing rhizosphere processes towards increasing nutrient use efficiency and crop productivity. Future food security faces greater challenges than ever before. There is no simple solution to delivering increased crop productivity while increasing resource use efficiency and protecting environmental quality.

In this review, we have focused on root/rhizosphere processes and management relative to theoretic and practical aspects, but a broad range of options including crop genetic improvement, agronomic technology extension and access to technologies by farmers needs to be pursued simultaneously.
Such a comprehensive solution will require a multidisciplinary approach to solve the issue of harmonizing the relationships between elevated crop productivity and increased nutrient use efficiency in a sustainable way.

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