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Research article

Dynamics in the rhizosphere and iron-uptake gene expression in peanut induced by intercropping with maize: Role in improving iron nutrition in peanut

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A B S T R A C T

The intercropping of maize with peanuts is an effective cropping practice. Indeed, peanut/maize intercropping reportedly improves the iron nutrition of peanuts in calcareous soils. The limited evidence available suggests that the improved Fe nutrition in intercropping is largely attributable to a rhizosphere effect of maize. In this study, the effects of peanut/maize intercropping on the Fe nutritional status of peanut associated with the dynamics of the rhizosphere processes and Fe uptake gene expression induced by the interaction of the two species at various growth days were investigated. The results suggest that an interspecific rhizosphere effect improves Fe nutrition in peanut, as shown by changes in the rhizosphere available Fe concentration, pH, and Olsen-P concentration, based on time-course changes in peanut–maize interaction. The increase in available Fe in the rhizosphere of peanut ranged from 0.2 to 2.64 mg kg^{-1}. The transition from the vegetative to reproductive stage was a key turning point in the time-course of changes in the rhizosphere processes in intercropping. There was more consistently positive effect of intercropping on peanut Fe nutrition after 53 days. Moreover, the expression of *AhFRO1* and *AhYSL1* was expressed at significantly higher level in intercropped peanuts compared to monocropped peanut at the vegetative stage, indicating a role for these genes in Fe improvement in intercropped peanuts. We conclude that the enhanced time-course changes in the rhizosphere processes and iron uptake gene expression with a consistent positive interspecific effect appear to be one of the mechanisms underlying the improved Fe nutrition in intercropped peanut plants.

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1. Introduction

Intercropping is of great importance for sustainable agro-ecosystems; through improved root interactions and the more effective use of resources, intercropping can improve the nutrition status and productivity of crops grown in low-input crop production systems (Li et al., 2007; Zhang et al., 2010). Compared with monocropping systems, intercropping is a promising strategy for the development of food production due to the lesser reliance on chemical fertilizer inputs (Zhang et al., 2010). In recent decades, research on intercropping has revealed an increase in the yields of maize and faba bean on phosphorus-deficient soils (Li et al., 2007). Song et al. suggested that intercropping significantly changed the microbiological biodiversities in the rhizosphere of wheat/faba bean and maize/faba bean intercropping systems, which may lead to increased crop yields (Song et al., 2007). In maize/wheat intercropping systems, the interaction of the two species showed marked effects on lateral development and increased the root length density (Li et al., 2006). The interspecific root interactions of wheat and chickpea affected the uptake and transport of several nutrients in both crops (Li et al., 2004). In tree-based intercropping systems, the growth and nutrient status of hybrid poplars were also improved (Rivest et al., 2009). It has been documented that peanut/maize intercropping is an effective and sustainable practice in the field that clearly improves the Fe nutrition of peanut plants (Zuo et al., 2000; Zuo and Zhang, 2008).

Fe is an essential element for plant growth; plants have developed two strategies in response to Fe limitation. Dicots and non-graminaceous monocots use a reduction-based strategy for the uptake of Fe in Fe deficiency. Under such conditions, Fe(III)-chelate is reduced to Fe(II) by ferric reductase oxidase (FRO) (Robinson

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et al., 1999), and the Fe(II) is then absorbed by the iron-regulated transporter (IRT) (Eide et al., 1996).

In contrast, grasses secrete mugineic acid-family phytosiderophores (MAs) (Römheld and Marschner, 1986) and absorb Fe(III)-MAs complexes using the yellow stripe 1 (YS1) transporter (Curie et al., 2001). In peanut plants, the *AhFRO1* and *AhIRT1* genes have been identified. Their expression is coordinately induced by Fe deficiency and regulated by intercropping with maize (Ding et al., 2009, 2010). Additionally, yellow stripe 1-Like (YSL) family members have been identified in peanut, and the *AhYSL1* protein in the epidermis of peanut roots transports Fe(III)-DMA. Thus, in a peanut/maize intercropping system the Fe(III)-DMA dissolved by maize may be absorbed directly by nearby peanuts (Xiong et al., 2013a). Peanut/maize intercropping not only significantly improves Fe nutrition in peanut plants, but also results in improvements in other nutrient concentrations, such as zinc (Zn), phosphorus (P), and potassium (K) (Inal et al., 2007).

Recently, some research groups have reported that the improvement in nutritional status in intercropping could be attributed to root interactions and rhizosphere effects induced by the two different plant species (Inal and Gunes, 2008; Gunes et al., 2007). The mechanisms of Fe uptake in monocropping and intercropping plants have been studied extensively in peanut plants in recent years (Ding et al., 2009, 2010). However, little is known about the time-course changes in the rhizosphere processes of peanut or the regulation of gene expression in the improvement of Fe status.

In this study, time-course changes in the rhizosphere induced by the interaction of the two crops in peanut/maize intercropping were investigated in calcareous soils under greenhouse experimental conditions. Moreover, we consider the possible regulatory effects in graminaceous species and their rhizosphere influence on gene expression in peanut plants and sought to explain the mechanisms underlying the Fe status improvement in peanuts at key growth stages in intercropping. Based on our research, we attempt to provide additional and feasible technologies and approaches for improving nutritional status and increasing the productivity of staple crops in low-input agricultural systems.

2. Materials and methods

2.1. Plant cropping design and growth conditions

Peanut (*Arachis hypogaea* L. cv. Luhua14) and maize (*Zea mays* L. cv. Nongda108) were used. Pot experiments were conducted in a typical iron-deficient calcareous sandy soil under greenhouse conditions. The soil was collected from 0 to 20-cm-depth soil samples in Beijing, China (39° 40′ N, 116° 15′ E). The properties of soil samples before fertilizer application were: organic matter 0.42%, total nitrogen 0.032%, available P (Olsen-P) 3.22 $\mu g\ g^{-1}$, NH_4OAc-K 42.9 $\mu g\ g^{-1}$, DTPA-Fe 2.71 $\mu g\ g^{-1}$, DTPA-Zn 0.46 $\mu g\ g^{-1}$, pH (in water) 8.3, and $CaCO_3$ 8.67%. The soil sample was amended with basal fertilizers [composition ($\mu g\ g^{-1}$ soil): N 100 (as $Ca(NO_3)_2 \cdot 4H_2O$), P 150 (as KH_2PO_4), K 100 (as KCl), Mg 50 (as $MgSO_4 \cdot 7H_2O$), and Zn 5 (as $ZnSO_4 \cdot 7H_2O$)].

Three cropping treatments with six replicates of each were used in the experiment. Six peanut plants and three maize plants were grown for the monocropping treatments. Three peanut plants with three maize plants were grown for the intercropping treatments. Maize plants were sown 12 days after peanuts germinated and emerged. The plants were grown under natural light conditions with 28–32 °C air temperature, 400–450 $\mu mol\ m^{-2}\ s^{-1}$ light intensity, and 70–75% relative humidity. During the experiment, soil water content was kept at approximately 80% of field capacity. After 34, 46, 53, 60, 69 and 76 days of peanut growth, plant samples of maize and peanut were harvested to assess the degree of Fe-deficiency chlorosis in the young leaves of the monocropped peanuts.

2.2. Plant analysis

Young leaves from peanuts in each treatment were washed several times with distilled water and then prepared for the assessment of HCl-extractable Fe ('active Fe'), according to the procedure of Takkar and Kaur (1984). The HCl-extractable Fe concentration was determined by inductively coupled plasma atomic emission spectrometry (ICP, Perkin–Elmer Optima 3300DV) and expressed as $\mu g.g^{-1}$ fresh weight (FW).

2.3. Soil sampling and analysis

Calcareous sandy soil, a typical Fe deficient soil was collected from Beijing, China (39°40′N, 116°15′E). When we get plant samples from the soil, a little soil could attach the root of plant, and this soil could be directly influenced by root activities. Therefore, the soil that remained adhering to the root surfaces of peanut and maize (30 g–40 g) was collected as rhizosphere soil. The changes in pH, the available Fe concentration (DTPA-Fe), the Olsen-P and total nitrogen concentrations were determined in the rhizosphere soil of peanut and maize. The pH value in the rhizosphere was determined using a pH meter (Peech, 1965). Briefly, a 10.0-g soil sample was placed in a 200-mL flask with 50 mL of distilled water and shaken for 3 min and then filtered. A 20-mL aliquot from the filtrate was used to determine the pH. The available P was extracted with 0.5 mol L^{-1} $NaHCO_3$ for 30 min NH_4OAc-K was determined by extracting the soil with 1 mol L^{-1} NH_4OAc for 30 min and was analyzed using a flame photometer (Chapman, 1965). Total nitrogen was determined by a semi-micro Kjeldahl digestion followed by ammonium distillation and titrimetric determinations (Bremner, 1965).

2.4. Measurement of ferric reductase activity

At each harvest, the fresh peanut plants were washed and then immersed in saturated $CaSO_4$ solution for 30 min. After washing, peanut plants were transferred to 200 mL of nutrient solution with 0.5 mM Fe(III)-EDTA, 0.01 M MES buffer (pH 6.0) and 0.2 mM ferrozine for a 2-h incubation. The absorbance of the solution at 520 nm was measured. Ferric reductase activity was calculated based on the absorbance and expressed as $nmol.g^{-1}$ fresh weight (FW) per h ($nmol\ g^{-1}\ FW\ h^{-1}$).

2.5. Quantitative real-time PCR

Total RNA was extracted from intercropped and monocropped peanut roots using the TRIzol reagent (Invitrogen) and treated with RNase-free DNase I (Takara) to remove genomic DNA contamination. The first-strand cDNA was synthesized with M-MLV reverse transcriptase (Promega). Quantitative real-time PCR was performed using the SYBR Green PCR Master Mix reagent (Applied Biosystems) and an ABI7500 Fast Real-Time PCR System (Applied Biosystems). The primers used were according to Xiong et al. (2013a), and peanut ubiquitin was used as an internal control.

2.6. Statistical analysis

All data were analyzed using the SPSS software, expressed as means of six replicates with standard deviations. The means were assessed by the independent-samples *t*-test method at the 5% probability level.

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