Proline-2'-deoxymugineic acid, active Fe chelator enhance peanut yield by integrated improving soil-plant Fe status at molecular and ecological level

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Abstract

Iron (Fe) deficiency restricts crop yields in calcareous soil. Thus, a novel Fe chelator, proline-2'-deoxymugineic acid (PDMA), based on the natural phytosiderophore 2'-deoxymugineic acid (DMA), was developed to solve the Fe deficiency problem. However, the effects and mechanisms of PDMA relevant to the Fe nutrition and yield of dicots grown under field conditions require further exploration. In this study, pot and field experiments with calcareous soil were conducted to investigate the effects of PDMA on the Fe nutrition and yield of peanuts. The results demonstrate that PDMA could dissolve insoluble Fe in the rhizosphere and up-regulate expression of the yellow stripe-like family gene *AhYSL1* to improve the Fe nutrition of peanuts. Moreover, the chlorosis and growth inhibition induced by Fe deficiency were significantly diminished. Importantly, under field conditions, the peanut yield and kernel micronutrition were notably promoted by PDMA application. Our results indicate that PDMA promotes the dissolution of insoluble Fe and a rich supply of Fe in the rhizosphere, increasing yields through integrated improvements in soil–plant Fe nutrition at the molecular and ecological levels. In conclusion, the efficacy of PDMA for improving the Fe nutrition and yield of peanut indicates its outstanding potential for agricultural applications.

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Abstract

Iron (Fe) deficiency restricts crop yields in calcareous soil. Thus, a novel Fe chelator, proline-2'-deoxymugineic acid (PDMA), based on the natural phytosiderophore 2'-deoxymugineic acid (DMA), was developed to solve the Fe deficiency problem. However, the effects and mechanisms of PDMA relevant to the Fe nutrition and yield of dicots grown under field conditions require further exploration. In this study, pot and field experiments with calcareous soil were conducted to investigate the effects of PDMA on the Fe nutrition and yield of peanuts. The results demonstrate that PDMA could dissolve insoluble Fe in the rhizosphere and up-regulate expression of the yellow stripe-like family gene*AhYSL1* to improve the Fe nutrition of peanuts. Moreover, the chlorosis and growth inhibition induced by Fe deficiency were significantly diminished. Importantly, under field conditions, the peanut yield and kernel micronutrition were notably promoted by PDMA application. Our results indicate that PDMA promotes the dissolution of insoluble Fe and a rich supply of Fe in the rhizosphere, increasing yields through integrated improvements in soil–plant Fe nutrition at the molecular and ecological levels. In conclusion, the efficacy of PDMA for improving the Fe nutrition and yield of peanut indicates its outstanding potential for agricultural applications.

Keywords

Proline-2'-deoxymugineic acid, peanut, iron deficiency, yield, iron fertilizer

Abbreviation

DMA, 2'-DeoxyMugineic Acid

dps, days post sowing

DTPA, DiethyleneTriaminePentaacetic Acid

EDTA-Fe, Fe-EthyleneDiamine-N ,N ,N' ,N' -Tetraacetic Acid complex

Fe, iron

FIT, FER-like Iron deficiency-induced Transcription factor

IRT, Iron-Regulated Transporter

MAs, Mugineic Acid family phytosiderophores

NRAMP, Natural Resistance-Associated Macrophage Protein

PDMA, Proline-2'-DeoxyMugineic Acid

PDMA-Fe, Fe-Proline-2'-DeoxyMugineic Acid complex

SPAD, Soil and Plant Analyzer Development

TEA, TriEthanolAmine

YSL, Yellow Stripe-like

YS, Yellow Stripe

Introduction

Iron (Fe), an indispensable microelement for plants, is essential for many physiological functions, including oxidation–reduction system functions, chlorophyll synthesis, and respiration (Broadley et al., 2012, Kobayashi et al., 2019). Although Fe is abundant in soil, the amount available for plants is limited because Fe always exists as insoluble complexes (Marschner and Rengel, 2012, Vasconcelos et al., 2017, Zhang et al., 2019). Moreover, the availability of Fe is significantly lower in soil with a high pH, such as the calcareous soil of northern China (Abadía et al., 2011, Zuo and Zhang, 2011).

Based on their different response mechanisms to Fe deficiency, plants can be divided into Strategy I and Strategy II plants (Kobayashi and Nishizawa, 2012, Riaz and Guerinot, 2021). Strategy I plants, including non-grass monocots and dicots, can increase Fe availability in the rhizosphere and reduce Fe^{3+} to Fe^{2+}via

ferric reductase under Fe-deficient conditions (Li and Lan, 2017, Rajniak et al., 2018). Fe^{2+} is then transported into roots via Fe-regulated transporter (IRT) proteins and natural resistance-associated macrophage protein (NRAMP), which is regulated by FER-like Fe deficiency-induced transcription factor (FIT) (Vert et al., 2002, Yuan et al., 2008, Dai et al., 2018). In contrast, Strategy II plants, including gramineous monocots, secrete mugineic acid family phytosiderophores (MAs) into the rhizosphere to chelate Fe (Conte and Walker, 2011, Grillet and Schmidt, 2019), and the MA–Fe complex is taken up by plants via yellow stripe (YS) transporters (Curie et al., 2009, Conte and Walker, 2012, Tripathi et al., 2018).

The Strategy I plant response to Fe deficiency is restricted to high pH conditions (Romheld and Marschner, 1986) and occurs frequently in calcareous soil (Zuo and Zhang, 2009, Zuo and Zhang, 2011). Recent studies have revealed that Strategy I plants can utilize the phytosiderophore 2'-deoxymugineic acid (DMA) secreted by Strategy II plants to improve Fe nutrition (Suzuki et al., 2016, Astolfi et al., 2020). The YS homologous transporter, related to DMA uptake, is also found in Strategy I plants (Xiong et al., 2013). However, in agricultural production, DMA is impractical for use as an Fe fertilizer to improve the Fe nutrition of Strategy I plants because of its easy degradation and high cost of synthesis (Takagi et al., 1988, Suzuki et al., 2021).

Recently, a novel Fe-chelating agent, proline-2'-deoxymugineic acid (PDMA), was synthesized based on the structure of DMA (Suzuki et al., 2021). PDMA is much more stable than DMA, and the cost of synthesis is lower (Kratena et al., 2021, Suzuki et al., 2021). Moreover, PDMA has been shown to improve the Fe nutrition of various plants in hydroponic culture and calcareous substrates (Suzuki et al., 2021, Ueno et al., 2021), thus revealing the great potential of PDMA as a novel biological Fe fertilizer. However, the effect of PDMA on improving the Fe nutrition and yield of crops remains unclear under field conditions.

Peanut (*Arachis hypogaea*), an important oil crop, is planted widely in northern China, and its yield and quality are greatly restricted by Fe deficiency (Zuo and Zhang, 2009, Roriz et al., 2020). To correct Fe deficiency in crops, chemosynthetic Fe-chelator complexes, such as the Fe-ethylenediamine-*N* ,*N* ,*N'* ,*N'* -tetraacetic acid complex (EDTA–Fe), are commonly used in modern agriculture as an Fe fertilizer (Abadía et al., 2011, Nadal et al., 2012). Due to the high pH in calcareous soil, Fe fertilizer is easily fixed in the soil after application. Nonetheless, PDMA has a greater demonstrated ability to improve Fe nutrition in rice and cucumber (Suzuki et al., 2021, Ueno et al., 2021). However, the influence of PDMA on the Fe nutrition and yield of peanuts grown in calcareous soil requires further investigation.

In the present study, we evaluated the effect of neotype Fe fertilizer-PDMA on peanut Fe nutrition and examined its mechanism at the molecular and ecological levels. We investigated the effects of PDMA using pot and field trials and revealed that PDMA could improve Fe nutrition effectively, thus promoting the yield of peanuts under field conditions. These results suggest great application prospects for PDMA in agricultural systems.

Materials and Methods

Preparation of the treatments

PDMA was synthesized and supplied by the Aichi Steel Corp. (Japan) as described in a previous report (Suzuki et al., 2021). The PDMA–Fe complex was prepared as described in a recent work (Ueno et al., 2021). First, we mixed 2.47 M $FeCl_3$ with 10 mM PDMA at a ratio of 2:1 and then adjusted the pH to 7.0 with 0.5 M NaOH. Next, the solution was incubated for 1 h at 50°C and centrifuged for 3 min at 15,000 rpm. Finally, the mixture was filtered with a 0.22 μm syringe filter. The PDMA and PDMA–Fe were stored at -20°C until use. EDTA–Fe (CAS No. 15708-41-5; Shanghai Macklin Biochemical Co., Ltd., China) was used as a positive control in the pot and field experiments.

Plant culture conditions

The cultivar of peanut used in the pot and field trials was Luhua 14. The pot assay was carried out in a greenhouse at China Agricultural University (Beijing, China). After germination for 2 days, six peanut seeds were transferred to each pot, each filled with 8 kg of calcareous soil. The soil pH was 7.5, and the available Fe was 3.61 $mg{\cdot}kg^{-1}$. The basic fertilizer contents ($mg{*}kg^{-1}$) were $Ca(NO_3)_2{*}4H_2O$, 10; KH_2PO_4, 150; KCl,

100; $MgSO_4*7H_2O$, 50; $CuSO_4*5H_2O$, 5; and $ZnSO_4*7H_2O$, 5. The treatments (PDMA, PDMA–Fe, and EDTA–Fe) were prepared as 40 μM aqueous solutions. The treatments (300 ml) were irrigated into the peanut rhizosphere of each pot at 30, 48, 65, and 83 days post-sowing (dps), which matched the flowering stage, early pod-bearing stage, late pod-bearing stage, and fruit-ripening stage of peanut, respectively. The same amount of water was irrigated as a control. The soil plant analysis development (SPAD) value in expanded young leaves was recorded using a chlorophyll meter (SPAD-502Plus; Konica Minolta, Japan) at 7 days after treatment application. At 90 dps, we took photographs of the peanuts under the different treatments and then harvested the peanuts. A portion of the fresh young leaves was collected to determine the active Fe concentration. The fresh root was divided into two parts. One part was used to measure the activity of ferric reductase, and the other part was stored in a -80°C freezer to examine gene expression. Rhizosphere soil was collected to determine the available Fe content. The other parts of the peanut plants were dried in a drying oven (ULM700; Memmert, Germany) until constancy and then weighed with a balance.

The field experiment was conducted in the village of Xichang in Beijing, China (116°10' E, 39°10' N). The average temperature from May to September is 22.9°C, and the annual precipitation is 603 mm. The soil in the field is a calcic Cambisol. The soil pH, available Fe, total nitrogen (N), available phosphorus (P), and available potassium (K) were 7.7, 3.0 $mg{\cdot}kg^{-1}$, 1.4 $g*kg^{-1}$, 112.3 $mg*kg^{-1}$, and 157.2 $mg*kg^{-1}$, respectively. Organic fertilizer (N:P:K contents of 25.8 $g*kg^{-1}$, 5.7 $g*kg^{-1}$, and 17.1 $g*kg^{-1}$, respectively) was applied at 20 $t*hm^{-1}$ before peanut planting. The plant spacing was 30 cm, and the row spacing was 60 cm. The treatments in the field trial were the same as those in the pot trial, with three districts used in each treatment. Each district contained 16 holes, and two peanut kernels were planted in each hole. The treatments were prepared as 40 μM aqueous solutions, and 100 ml of solution was irrigated into the peanut rhizosphere in each hole. The same amount of water was irrigated as a control. In the field condition, the treatments were added four times during the growth stage at 30, 52, 72, and 93 dps, matching the flowering stage, early pod-bearing stage, late pod-bearing stage, and fruit-ripening stage of peanut. The SPAD value in expanded young leaves was recorded at 67 and 107 dps using a chlorophyll meter (SPAD-502Plus; Konica Minolta). Eight SPAD values were measured in each district. At 107 dps, the peanut plants were photographed and then harvested. A portion of the fresh young leaves was collected to determine the active Fe concentration. The fruits of the peanuts were harvested, dried until constant weight, and then the yield, kernel yield, fruit weight per plant, and fruit number per plant were determined.

Active Fe in young leaves

Fresh peanut leaves from each pot or district were mixed, and 1 g of leaf was taken and mixed with 10 ml of 1 M hydrochloric acid. The supernatant was shaken for 5 h at 150 rpm and then filtered with filter paper. The Fe concentration was measured by inductively coupled plasma–optical emission spectrometry (ICP-OES) using a 7300DV system (Perkin Elmer, USA).

Available Fe in soil

After the rhizosphere soil was air-dried, 10 g of soil was weighed and added to 20 ml of diethylenetriaminepentaacetic acid (DTPA) extracting agent, containing 0.005 M DTPA (CAS No. 67-43-6), 0.01 M $CaCl_2$, and 0.1 M triethanolamine (TEA; CAS No. 102-71-6). Then, the mixture was shaken for 2 h at 180 rpm at 25°C. Subsequently, the solution was filtered and the Fe concentration in the filtrate was measured by ICP–OES.

Ferric reducibility assay

The fresh peanut roots were washed twice with distilled water, weighed, and then immersed in a reagent consisting of 0.4 mM 2,2'-dipyridyl (CAS No. 366-18-7) and 0.1 mM EDTA-Fe for 2 h without light (100 ml of solution per root). Then, the absorbance of the reaction solution was measured at 520 nm using an ultraviolet spectrophotometer (T2600; Yoke Instrument Co., Ltd., China). Ferric reductase activity was calculated with the formula below:

Ferric reductase ($\mu mol{\cdot}g^{-1}*t^{-1}$) = A_{520} / (FW * 8650) * 10^6,

where FW is the fresh weight of the root, and 8650 is the molar absorbance of Fe(II)–dipyridyl ($L*mol^{-1}*cm^{-1}$).

Real-time quantitative ***reverse transcription-PCR***

TRIzol reagent (Invitrogen, USA) was used to extract total RNA from peanut root. Then, RNase-free DNase I (Takara, Japan) was used to remove genomic DNA contamination. cDNA was synthesized using ReverTra Ace Reverse Transcriptase (Toyobo, Japan). SYBR Premix Ex Taq (Perfect Real Time) reagent (Takara, Japan) and a real-time PCR detection system (CFX96; Bio-Rad, USA) were used to perform real-time quantitative PCR. The primers used for real-time quantitative PCR are listed in Table S1.

Micronutrition in the kernel

After oven-drying to a constant weight, the kernel was triturated. The triturations from peanuts grown in each district were mixed and used as one repetition. After adding 6 ml of 15 M nitric acid, the trituration was stored overnight. Then, 2 ml of 30% H_2O_2 was added and the mixture was digested using a microwave oven high-pressure digestion system (Mars 6 Classic; CEM Corp., USA). The micronutrient contents in the kernel were determined by ICP–OES.

Statistical analysis

All data were analyzed using SPSS 23.0 software (SPSS Inc., USA). The least significant difference test was used to indicate significant differences. The ggplot2 package in R software was used to draw illustrations.

Results

PDMA enhancement of peanut Fe nutrition in calcareous soil

To investigate the effect of PDMA on peanut plants, we applied a PDMA or PDMA–Fe solution into the peanut rhizosphere in a pot assay. Application of PDMA or PDMA–Fe significantly enhanced plant growth and the SPAD value in young peanut leaves (Fig. 1). At 90 dps, the PDMA and PDMA–Fe treatments resulted in a higher dry-mass weight of the shoot; it was increased by 51.9% and 44.0% compared with the control, respectively. These two treatments produced slightly higher results than did the EDTA–Fe treatment, although the differences were not significant (Fig. 1b).

The application of PDMA or PDMA–Fe had no effect on the SPAD value of young leaves compared with the control at 40 dps (flowering stage) (Fig. 1c). At 55 dps (early pod-bearing stage), increases in the SPAD value of young leaves of 20.4% and 22.6% under PDMA and EDTA–Fe application compared with the control, respectively, were observed. Moreover, at 72 dps (late pod-bearing stage), the SPAD values of young leaves were increased greatly by 51.6%, 52.8%, and 60.5% compared with the control following PDMA, PDMA–Fe, and EDTA–Fe application, respectively. Positive effects on the SPAD value of young leaves were also observed at 90 dps (fruit-ripening stage) following the PDMA, PDMA–Fe, and EDTA–Fe treatments, which showed enhancements of 42.7%, 40.8%, and 59.2%, respectively. In terms of peanut growth, PDMA and PDMA–Fe diminished chlorosis of the leaves and promoted plant growth. These positive effects were similar to those of traditional Fe fertilizers.

Enhancement of Fe availability by PDMA in the rhizosphere of peanut

The effects of PDMA on the Fe levels in peanut plants and the peanut rhizosphere are shown in Fig. 2. Plants treated with PDMA and PDMA–Fe displayed higher active Fe concentrations in young leaves, increased by 54.5% and 48.7% compared with the control, respectively, and these two treatments produced slightly higher results than did treatment with EDTA–Fe (Fig. 2a). Moreover, PDMA and PDMA–Fe significantly enhanced the level of available Fe in the rhizosphere by 25.5% and 19.1%, respectively; in contrast, Fe availability in the rhizosphere was not influenced by EDTA–Fe (Fig. 2b). The results above indicate improvements in the availability of soil Fe and Fe nutrition in peanut plants grown in calcareous soil due to PDMA or PDMA–Fe treatment.

Inhibition of ferric reductase activity and **AhIRT1*expression by PDMA application***

The physiological and underlying molecular responses to Fe deficiency in roots were inhibited following PDMA application. As shown in Fig. 3a, the three treatments greatly reduced ferric reduction activity compared with the control, and the plants treated with PDMA–Fe exhibited a lower level than plants treated with PDMA and a higher level than plants treated with EDTA–Fe. Additionally, *AhIRT1* expression in roots was decreased by 58%, 55%, and 56% following treatment with PDMA, PDMA–Fe, and EDTA–Fe compared with the control, respectively (Fig. 3b). These results indicate that the available Fe level in the rhizosphere was much higher following PDMA, PDMA–Fe, and EDTA–Fe treatment than in the control plants.

Up-regulation of **AhYSL1** ***expression in root by PDMA application***

The expression of Fe transporters under the different treatments is displayed in Fig. 4. *AhYSL1* expression in roots treated with PDMA and PDMA–Fe was 1.8-fold and 2.5-fold the expression in the control, respectively, but no difference was detected with EDTA–Fe treatment (Fig. 4a). However, no significant differences in *AhFIT* and*AhNRAMP1* expression were detected (Fig. 4b, c). These results show that PDMA application promoted Fe absorption by roots, as represented by up-regulated AhYSL1 transporter expression (rather than AhFIT or AhNRAMP1 transporter expression).

Enhancement of peanut Fe nutrition under field conditions by PDMA

The effect of PDMA on peanut Fe nutrition was investigated further under field conditions (Fig. 5). As shown in Fig. 5a, PDMA treatment resulted in a 6.7% increase in the SPAD value of young leaves compared with control plants at 67 dps (pod-bearing stage). At 107 dps (fruit-ripening stage), peanut plants treated with PDMA, PDMA–Fe, and EDTA–Fe exhibited greatly promoted SPAD values in young leaves, higher by 10.4%, 11.8%, and 10.6%, respectively, compared with the control. Moreover, significant increases of 50.2%, 50.3%, and 45% were found in the active Fe concentrations of young leaves following PDMA, PDMA–Fe, and EDTA–Fe treatment, respectively (Fig. 5b). PDMA and PDMA–Fe treatment produced slightly higher increases than EDTA–Fe treatment, but the differences were not significant. These results demonstrate the great capabilities of PDMA and PDMA–Fe in relieving Fe deficiencies in peanut plants under field conditions.

Enhancement of peanut yield in calcareous soil by PDMA

The effect of PDMA on peanut yield was investigated in detail; the results are displayed in Table 1. Peanut plants treated with PDMA, PDMA–Fe, and EDTA–Fe exhibited yield enhancements compared with the control of 30.2%, 33.4%, and 26.1%, respectively. Peanut plants treated with PDMA–Fe had the highest kernel yield, followed by PDMA-Fe and EDTA–Fe-treated peanut plants, with enhancements compared to the control of 38.2%, 33.9%, and 27.1%, respectively. PDMA and PDMA–Fe treatment produced enhancements in peanut yield and kernel yield of 3.3% and 5.8% and 5.3% and 8.7% in comparison with EDTA–Fe treatment, respectively. Moreover, higher plump fruit weights and plump fruit numbers per plant were obtained with PDMA, PDMA–Fe, and EDTA–Fe application. These results indicate that PDMA could significantly promote peanut yields under field conditions.

Accumulation of micronutrition in the kernel following PDMA application

The effects of PDMA on micronutrition in the kernel are displayed in Fig. 6. The Fe content in the kernel was significantly promoted by PDMA and PDMA–Fe treatment, with increases of 36.4% and 47.1%, respectively (Fig. 6a). Compared with the control, the application of PDMA and PDMA–Fe enhanced the zinc content in peanut kernels by 38% and 48.4%, respectively (Fig. 6b). Moreover, PDMA and PDMA–Fe treatment resulted in higher levels of manganese and copper (Fig. 6c, d). The micronutrition in peanut kernel was significantly promoted by PDMA, and the effects were significantly higher than those obtained with EDTA–Fe treatment.

Discussion

Recently, PDMA, an effective Fe chelator, was synthesized based on the structure of the phytosiderophore DMA (Suzuki et al., 2021). PDMA, with low synthesis costs and high stability, was proven to improve Fe nutrition in rice and cucumber under conditions of hydroponic culture and calcareous substrates (Suzuki et

al., 2021, Ueno et al., 2021). In this study, positive effects of PDMA on Fe nutrition and peanut yields were demonstrated in calcareous soil under field conditions.

The present study revealed that the application of PDMA significantly corrected Fe deficiency in pot and field trials (Fig. 2, Fig. 5). Consistent with the accumulation of Fe, because Fe is a vital element involved in chlorophyll synthesis (Kobayashi et al., 2019), the SPAD values were enhanced substantially by PDMA application (Fig. 1, Fig. 5). The growth of the PDMA-treated peanut plants was therefore promoted (Fig. 1). Similar increases were found in rice and cucumber (Suzuki et al., 2021, Ueno et al., 2021). Importantly, our work produced the novel finding that PDMA can increase the yield and kernel micronutrition of peanuts (Table 1, Fig. 6), implying the great ability of PDMA to improve the production and quality of plants under Fe-limited field conditions.

PDMA resulted in higher levels of dissolved Fe in the rhizosphere than did EDTA–Fe, but the improvement in peanut Fe nutrition between these treatments was not significantly different (Fig. 2, Fig. 5). These results suggest that PDMA can chelate insoluble Fe in soil to improve Fe nutrition in comparison to traditional Fe fertilizers without any exogenous Fe supplementation, which realizes sustainable utilization of the Fe in soil (Colombo et al., 2014). This type of metal-free fertilizer effectively utilizes the residual nutrients in native soil and is conducive to the development of sustainable agriculture (Bouis and Welch, 2010).

Another mechanism by which PDMA may increase the Fe nutrition in peanut is that PDMA–Fe complexes may be taken up directly by roots via AhYSL1. A previous study indicated that PDMA can trigger YS family gene expression in Strategy II plants (Suzuki et al., 2021). In the present study, expression of the YS homolog *AhYSL1* in peanut root was up-regulated by PDMA (Fig. 4), suggesting that PDMA–Fe complexes might be directly assimilated by roots. Similar characteristics were found for DMA–Fe, which was proven to be taken up via the YSL transporter in both Strategy I and Strategy II plants (Xiong et al., 2013, Schenkeveld et al., 2014). Therefore, the absorption of PDMA–Fe, instead of regulation via *AhNRAMP1* and *AhFIT* , might be an important pathway for improving the Fe nutrition of peanut (Fig. 4). Additionally, higher Fe levels in Strategy I plants down-regulate the capacity of ferric reductase and the expression of *AhIRT1* (Martin-Barranco et al., 2020, Riaz and Guerinot, 2021). Similarly, the Fe uptake process in peanut root was decreased significantly (Fig. 3). Overall, PDMA improved peanut Fe nutrition by increasing Fe availability and up-regulating the absorption of PDMA–Fe. As an effective biostimulant, PDMA has great potential for the biofortification of plant growth, yields, and kernel micronutrition.

Chemosynthetic chelate–Fe, as represented by EDTA–Fe, is commonly used to improve the Fe nutrition of plants in the field (Abadia et al., 2011, He et al., 2013). However, chemosynthetic chelate–Fe is expensive and thus generally applied only to cash crops (Briat et al., 2015). Moreover, the residual chemosynthetic chelator does not degrade easily in the soil. Biological Fe fertilizers, such as humic acid–Fe and amino acid–Fe, have therefore been applied widely in the field in recent years to protect the soil environment (Saini et al., 2016). Nevertheless, because of the instability of biological Fe fertilizers in soil, the effect on plant Fe nutrition is limited, especially in calcareous soil (Briat et al., 2015). The neotype Fe chelator PDMA has been proven more stable than biological Fe fertilizers. Additionally, the biodegradability of PDMA can prevent the problem of environmental pollution caused by chemosynthetic chelate–Fe (Suzuki et al., 2021).

In conclusion, the novel Fe fertilizer PDMA can dissolve insoluble Fe in the rhizosphere and up-regulate *AhYSL1* expression to improve Fe nutrition in peanut and thus plant growth. Importantly, under field conditions, PDMA enhanced the yield and kernel micronutrition of peanuts significantly (Fig. 7). Our results demonstrate the excellent potential of PDMA for wide use as an Fe fertilizer and biostimulant in agriculture.

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Author contribution

M. Suzuki supplied PDMA. T. Wang and Y. Zuo conceived and designed the study. T. Wang, Q. Lu, S. Lang, K. Wang, and L. Niu performed the experiments. T. Wang and N. Wang analyzed the data and finished this manuscript. Y. Zuo and M. Suzuki revised this manuscript. Y. Zuo provided funding for this work as the corresponding author. All authors approved the manuscript.

Data availability

The main data supporting the finding of this study are available within the paper and

its supplementary material.

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