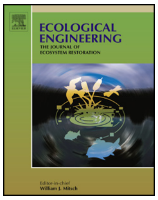
Ecological Engineering 95 (2016) 64–72

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng



Arbuscular mycorrhiza improved phosphorus efficiency in paddy fields

Shujuan Zhang[a,*], Li Wang[b,*], Fang Ma[b], Xue Zhang[b], Dafang Fu[a]

[a] *Department of Municipal Engineering, School of Civil Engineering, Southeast University, Nanjing, 210096, China*
[b] *State Key Laboratory of Urban Water Resource and Environment, School of Municipal and Environmental Engineering, Harbin Institute of Technology, Harbin, 150090, China*

ARTICLE INFO

Article history:
Received 12 August 2015
Received in revised form 3 May 2016
Accepted 14 June 2016
Available online 1 July 2016

Keywords:
Phosphorus acquisition efficiency
Arbuscular mycorrhizal fungi
Yield
Phosphorus uptake
Phosphorus use efficiency
Rice

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) were supposed to improve phosphorus (P) efficiency in paddy fields. Our aim was to investigate the roles of AMF inoculation in increasing P acquisition efficiency (PAE) by cutting down P loss and in enhancing P use efficiency (PUE) via optimizing shoot P investment. A field experiment with two factors was carried out in northeast of China: six fertilizer levels were provided, inoculation with *Glomus mosseae* was either conducted or not at each fertilizer level. We investigated P loss during the rice growing season while P uptake and investment, biological and economic yields of rice were estimated at maturity. Then, we calculated recovery efficiency (RE), utilization efficiency (UE) and agronomic efficiency (AE) for PAE and physiological efficiency (PE) and agrophysiological efficiency (APE) for PUE. Both apparent and balanced values of these indicators were calculated. In addition, relationships of balanced PAE—P loss and balanced PUE—P investment were investigated for the two sets of plants. We found that AMF inoculation improved root colonization and the economic yield but decreased the biological yield and seasonal P loss. Inoculation led to more P allocated to panicles but less to stems and leaves, without affecting shoot P uptake. We also found that the apparent RE, UE and AE were smaller in inoculated treatments while greater apparent PE and balanced AE and APE was observed in inoculated treatments. Additionally, P loss of paddy fields decreased exponentially as balanced PAE increased and inoculation reduced P loss, without affecting balanced PAE. For the two sets of plants, balanced PE was negatively correlated with shoot P invested in panicles but positively with shoot P invested in stems. Furthermore, inoculation did not significantly altered the relationship between balanced PE and shoot P invested in panicles and stems. Conclusively, our study highlights the importance of AMF inoculation in improving P efficiency of rice production.

1. Introduction

As there are limits to global rock phosphate reserves, increasing phosphorus (P) efficiency is vital to maintain current crop productivity (Veneklaas et al., 2012). Currently, excessive P fertilization is still common in Chinese agricultural systems, leading to P loss from farmlands and contributing largely to water pollution (Cao and Zhang, 2004; Ouyang et al., 2012). In addition, substantial increases in crop productivity are required to ensure food security in coming decades due to the rising population. To alleviate water pollution and achieve food security, crops are expected to (i) take up more P from the environments under given fertilization, *i.e.* exhibiting higher P acquisition efficiency (PAE); and (ii) achieve higher biological and economic yields based on given P acquired, *i.e.* showing higher P utilization efficiency (PUE).

There are two approaches to quantify PAE: the apparent and balanced approach (Johnston and Syers, 2009). For any approach, PAE can be calculated based on P uptake, biological and economic yields, indicated by recovery efficiency (RE), utilization efficiency (UE) and agronomic efficiency (AE), respectively (Table 1). The apparent PAE could be considered as the efficiency of P uptake from P fertilizer while the balanced PAE represented that from both soil and fertilizer (Johnston and Syers, 2009; Veneklaas et al., 2012; Fageria, 2014). Arbuscular mycorrhizal fungi (AMF) were hypothesized to enhance PAE of plants via constructing AMF-crop symbiosis (Vance, 2001; Maiti et al., 2011, 2012) as the external hyphae of AMF could fulfill and even surpass the functions of root architectures in P uptaking (Sims and Sharpley, 2005). However, other researchers

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* Corresponding authors.
E-mail addresses: zhangshujuan525@sina.com (S. Zhang), wli@hit.edu.cn (L. Wang).

http://dx.doi.org/10.1016/j.ecoleng.2016.06.029

Table 1
Definitions and calculations P-acquisition efficiency and P-use efficiency (Johnston and Syers, 2009; Veneklaas et al., 2012; Fageria, 2014).

	Traits	Descriptors	Definitions	Formulas for calculation
PAE	Apparent PAE	Apparent RE	relative quantity of P uptake per unit of P applied	Apparent RE (%) = (Pi- P0) × 100/PI
		Apparent UE	relative biological yield per unit of P applied	Apparent UE (kg kg^{1}) = (Bi- B0)/PI
		Apparent AE	relative economic yield per unit of P applied	Apparent AE (kg kg^{1}) = (Ei- E0)/PI
	Balanced PAE	Balanced RE	absolute quantity of P uptake per unit of P applied	Balanced RE (%) = Pi × 100/PI
		Balanced UE	absolute biological yield per unit of P applied	Balanced UE (kg kg^{1}) = Bi/PI
		Balanced AE	absolute economic yield per unit of P applied	Balanced AE (kg kg^{1}) = Ei/PI
PUE	Apparent PUE	Apparent PE	relative biological yield per unit of P aquire	Apparent PE (kg kg^{1}) = (Bi- B0)/(Pi-P0)
		Apparent APE	relative economic yield per unit of P aquire	Apparent APE (kg kg^{1}) = (Ei- E0)/(Pi-P0)
	Balanced PUE	Balanced PE	absolute biological yield per unit of P aquire	Balanced PE (kg kg^{1}) = Bi/Pi
		Balanced APE	absolute economic yield per unit of P aquire	Balanced APE (kg kg^{1}) = Ei/Pi

Abbreviations: PAE, P-acquisition efficiency; PUE, P-use efficiency; RE, recovery efficiency; UE, utilization efficiency; AE, agronomic efficiency; PE, physiological efficiency; APE, agrophysiological efficiency; Pi/Bi/Ei, P uptake/biological yield/economic yield when the fertilizer level is 'i' (i = 20, 40, 60, 80 and 100% of the local norm of fertilizer); P0/B0/E0, P uptake/biological yield/economic yield when the fertilizer level is '0% of the local norm of fertilizer'; PI, P applied at each fertilizer level.

predicted that AMF might reduce PAE by changing root architecture as they found that there was a complementary relationship between root architecture and AMF colonization in soybean (Wang et al., 2011). Although the above assumptions of the effect of AMF inoculation on PAE were inconsistent, no study has systematically quantified the role of AMF inoculation in regulating PAE calculated by the two approaches, indicated by RE, UE and AE.

Besides PAE, PUE is another bottleneck for further improvements in P efficiency (Wang et al., 2010). Both apparent and balanced values of PUE can be calculated based on biological and economic yields, indicated by physiological efficiency (PE) and agrophysiological efficiency (APE), respectively (Johnston and Syers, 2009; Veneklaas et al., 2012; Fageria, 2014) (Table 1). Previous study reported that AMF inoculation increased P uptake (*i.e.* the outcome of P concentration by biomass) and biological yield of acerola seedlings in greenhouse conditions (Balota et al., 2011). Similar effect was also found in rice at the harvesting stage (Solaiman and Hirata, 1997). Besides P uptake and biological yield, economic yields were improved by AMF inoculation in our previous research (Zhang et al., 2014). However, contrasting results were reported when the effects of inoculation on P uptake, biological and economic yields were considered together. On one hand, the positive effects of AMF on P uptake, biological and economic production might not be coupled with each other. Specifically, AMF were found to increase P uptake irrespective of biological yield (Hetrick et al., 1996; Smith et al., 2003). On the other, researchers predicted that the effects of AMF on P uptake and biological yield were linked with each other as the effect of AMF on bilogical yield was based on the altered P uptake due to AMF colonization (Grimoldi et al., 2005). As one of significant indicators of P efficiency, PUE was calculated based on P uptake, biological and economic yields. Therefore, the responses of PUE to AMF inoculation would provide an idea on whether the effects of AMF on plant performances (*i.e.* P uptake, biological and economic yields) were coupled with each other.

Phosphorus (P) in fertilizers applied could be taken up by crops, retained in soil or lost with runoff water. Soil P retention was affected by clay and organic matter content, Fe- and Al-oxides content, Ca active species content, cation exchange capacity, pH colloid specific, and so on (Sun et al., 2012). Given that there was not much variation in these soil characteristics, we assumed that the P retention was relatively stable. Based on this, someone might hypothesize that there was a negative relationship between PAE and P loss and AMF inoculation altered PAE by changing P loss of paddy fields. Besides the relationship between PAE and P loss, PUE might be correlated with P allocation as a higher PUE was mainly attributed to efficient re-translocation and re-use of the stored P in plants. This suggested that plants grown in changing environments could optimize P investment in these organs to satisfy their functions physiologically. However, whether PUE is coupled with indicators of P allocation and whether AMF inoculation improve PUE through optimizing P allocation, are not clear so far.

In our study, we systematically estimated the effects of AMF inoculation on indicators of PAE and PUE and the relationships of PAE—P loss and PUE—P allocation in rice (*Oryza sativa* L.). Specifically, we address the following questions: (1) are the PAE and PUE of rice improved by AMF inoculation? If so, (2) does AMF inoculation increase PAE *via* cutting down P loss; and (3) does AMF inoculation enhance PUE by optimizing shoot P investment?

2. Methods and materials

2.1. Site description, experimental design and inoculation

Our study was carried out on the lower reaches of Lalin River (45°13.82′N, 126°22.61′E), northeast of China. The organic matter, hydrolysable nitrogen (N), available phosphorus (P) and available potassium (K) of the paddy soil were 26 g kg^{-1}, 125 mg kg^{-1}, 160 mg kg^{-1} and 18 mg kg^{-1}, respectively. Based on the agricultural practice for rice in the local area, 238 kg ha^{-1} of N, 105 kg ha^{-1} of P and 110 kg ha^{-1} of K were applied every year in this area.

There were two levels for inoculation: inoculated and non-inoculated treatments (indicated by +M and −M, respectively) while there were six fertilizer levels provided, that was, 0%, 20%, 40%, 60%, 80%, and 100% of the local norm of fertilizer supply. Phosphorus (P) and potassium (K) were applied as basal dressing while N fertilizer was applied four times, with 60% as basal dressing, 40% as top dressings. The basal dressing was a compound fertilizer (N, P_2O_3 and K_2O in ratio 16:17:12) while the first and third top dressings were ammonium sulphate, with the second top dressing was urea. We chose *Glomus mosseae* HDSF1 as our AMF isolate which was deposited in China General Microbiological Culture Collection Center (CGMCC no. 3012). The inoculum was produced with enclosed sterile culture method and the spore density of the inoculum was 33–35 g^{-1} and percentage of root length colonization (RLC) was 74.8%.

Rice seedlings were cultivated in a greenhouse for six weeks. In +M treatment, 250 g of AMF inoculum and 50 g of rice seeds were mixed with the air-dried soil, followed by 1 kg of air-dried soil to cover the seeds. In −M treatment, AMF inoculum was replaced with 250 g sterilized growth medium (soil diluted with sand and vermiculite with volume ratio of soil, sand and vermiculite 2:5:3) (Zhang et al., 2014). A split-plot design was used in our experiment with fertilization in main plots and inoculation in split plots. Soil sterilization was not conducted either for seedling cultivation or for transplantation so that this experiment was carried out in a natural soil. There were three replicates and the area of main plots was 25 m^{2} while each split plot covered an area of 1 m^{2}. A vertical geomembrane (extending 0.5 m above and below ground) was