Oryza Vol. 54 No. 3, 2017 (290-297)
DOI 10.5958/2249-5266.2017.00040.6

Understanding the AM fungal association in flooded rice under elevated CO_2 condition

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Received : 26 July 2017 Accepted : 27 October 2017 Published : 28 October 2017

ABSTRACT

Arbuscular Mycorrhizal fungi (AMF) exhibit multifunctional mutualistic symbiosis with plants. The beneficial effect of AMF has been exploited for most of the crop plants but its role in flooded rice cultivation particularly under elevated CO_2 is not much dissected. Most of the research findings revealed that, the higher dose of phosphorous fertilizer application limits the AMF colonization in crop plants. In view of above, the present study was conducted to understand whether recommended dose of phosphorous fertilizers have any negative effects on AMF association in flooded rice under elevated CO_2 condition. This experiment comprised of four treatments, which include three methods of AMF inoculation and an uninoculated control. The entire experiment was maintained at ambient and elevated CO_2 (550 ± 20 and 700 ± 20 ppm) in open top chamber. In general, the mycorrhizal root colonization and sporulation was 1.2-2.5 times higher in AMF inoculated treatments than uninoculated control. Among different methods of mycorrhizal application, transplanting of mycorrhized seedlings or mycorrhized seedlings along with basal application of AMF increased sporulation and AMF colonization by 32-69 % and 14-56%, respectively compared to uninoculated control after 60 days of planting. The grain phosphorous content was increased by 14.0 - 21.4 % in AMF inoculated treatments as compared to uninoculated control in both ambient and eCO_2 conditions. The present study revealed that, application of AMF along with recommended dose of fertilizers (80:40:40 NPK kg ha^{-1}) significantly improves mycorrhizal root colonization, sporulation and plant P uptake in anaerobic rice under ambient and elevated CO_2 condition.

Key words: *AM fungi, rice, elevated CO_2, root colonization, phosphorus uptake*

INTRODUCTION

Arbuscular Mycorrhizal Fungi (AMF) is a key component of soil microbiota and it comes under phylum Glomeromycota (Schubler et al., 2001) represents the most common, dynamic and widespread terrestrial plant symbiotic association. They are obligate soil fungi and exchanges mutual benefits with approximately 80% of terrestrial plant species including majority of agricultural crops. The AMF helps agricultural crops by improving soil structure, plant nutrition and disease management (Pozo and Azcon, 2007), soil health management, drought and salinity tolerance (Porcel, 2011; Auge et al., 2015) along with other ecosystem services in exchange with photosynthetic products (Smith and Read, 2008). The establishment of AMF richness in soil may provide a valid alternative to conventional fertilization particularly for phosphorous management. The AMF can overcome the limitations in plant growth caused by inadequate nutrient supply particularly phosphorus (Nouri et al., 2014). There are many scientific reports that, clearly stated the importance of AMF in solving P deficiency. AMF through its indirect mechanism causes changes in pH (Li et al., 2001), root exudation profile and make it favorable for profuse development of microbial community and enhances P solubilization .

For sustainable rice production, apart from adoption of modern scientific cropping sequences (Roy et al., 2011; Kumar et al., 2016), proper nutrient

management approach to ensure adequate supply of essential nutrients is highly essential. As rice demands huge amount of phosphorous (P), therefore in order to overcome the future P crisis for sustainable rice cultivation, AMF can be appreciated as a 'saviour for rice' cultivation. Presently phosphorous is becoming a limiting nutrient and by 2050, there will a vast P crisis globally. Most of the crop plants including rice require P for most of the cellular and physiological functions. Hence, knowledge on the interaction of rice with AMF will open a bright scope for developing AMF based bio-inoculants for rice under wide range of cultivation. Rice plants readily form mycorrhizal associations under upland conditions, but under submerged conditions its infection is rare due to the anoxic environment (Ilag et al., 1987). However, some reports have reported the AMF colonization under flooded conditions (Secilia and Bagyaraj, 1994a, 1994b; Solaiman and Hirata, 1996). However, there are only few studies providing an overview of the colonizing AMF in rice roots and there is still no clear picture of how the association may be exploited to benefit crop yield under adverse environmental conditions (Vallino et al., 2009). Now a day, increased attention is being given on the influence of rapid increase in atmospheric CO_2 concentration on nutrient cycling in ecosystems. Further understanding of how elevated CO_2 affects phosphorus acquisition and plant utilisation will be critical for "P" management to maintain ecosystem sustainability in P deficient regions (Fohse et al., 1988; Veneklass et al., 2012).

The research evidence indicated that, the change in earth's climate will eventually occur due to increase in "greenhouse" gases like CO_2 (IPCC, 2001). The CO_2 concentration in atmosphere has increased from 270 µL L^{-1} in 2009 to 394 µL L^{-1} in 2013 (Leakey et al., 2009; Goufo et al., 2014) and this concentration will accelerate with models predicting that CO_2 concentration will rise to 550 µL L^{-1} by middle of this century and up to 800 µL L^{-1} by end of this century (Long and Ort, 2010; Feng et al., 2014). Significant increase in phosphorus demand by plants is likely to happen under elevated CO_2 due to the stimulation of photosynthesis, and subsequent growth responses. But most of the research findings indicated that the beneficial effect of AMF will be more under phosphorous deficient conditions and higher level of fertilizers application drastically reduces their colonization and sporulation in many crop plants. In this backdrop, the present study was initiated to understand whether the recommended level of fertilizers for lowland rice cultivation under elevated CO_2 condition has any adverse effect on AMF association in rice.

MATERIALS AND METHODS

Experimental site

The experiment was performed at Open Top Chamber (OTC), which is exclusively setup to carry out experiments under elevated CO_2 at National Rice Research Institute, Cuttack (Latitude 20° 3'N, Longitude 85° 49' 60" E; 24 m above sea level). The climate of this area is comes under tropical climate with heavy rainfall during monsoon. The mean annual precipitation was around 1500 mm. The details of the experimental set up of the OTC is described in Kumar et al., 2017.

Soil sample collection and preparation

Soil samples (0-25 cm depth) were collected from the research farm of National Rice Research Institute, Cuttack, Odisha, India and these soils were used for pot culture experiment. The collected soil samples were thoroughly air dried in shade, pulverized, sieved through 2 mm sieve and then analyzed for initial chemical and AMF sporulation. The soil used for this experiment was sandy clay loam with the following properties *i.e.*, pH: 5.94, EC: 0.5 dSm^{-1}, available soil N: 0.0043%, available P: 11.5 kg ha^{-1}, K: 130 kg ha^{-1} and AMF sporulation of 2-3 spores g^{-1} soil. The organic carbon (Jackson, 1967), available nitrogen (Subbaiah and Asija, 1956), available phosphrous (Bray and Kurtz, 1945), available potassium (Jackson, 1967), pH (Piper, 1967), electrical conductivity (Black, 1965) and AMF sporulation (Gerdemann and Nicolson, 1963) were done by adopting standard methods.

Mass multiplication of AM fungi

The AM fungal spores were multiplied in sterile sand: soil mixture (1:1) by using Rhode grass (*Chloris gayana* Kunth) as a host plant. After 4 months, the top vegetative portion of Rhode grass was removed and the roots were thoroughly mixed with the substrate. The soil based AMF inoculum containing 78-80 spores g^{-1} soil was used for the study. The inoculum containing mixed AMF *i.e.*, *Funneliformis mosseae*,

Rhizophagus fasciculatus and *Rhizophagus intraradices* which were collected from Soil Microbiology Lab, Crop Production Division, ICAR-NRRI, Cuttack, India.

Experiment details

The rice seedlings (variety: Naveen) used in this experiment was produced in small plastic trays (45 cm length 30 cm width and 15 cm height) filled with soil. In this method, two type of seedlings were produced i) seedlings produced from unsterilized soil ii) mycorrhized seedlings were produced from unsterilized soil inoculated with AMF inoculums (@ 25 g per kg soil). The rice (variety Naveen) seeds were surface sterilized with 0.1% $HgCl_2$ and then washed repeatedly with sterile water to keep it free from pathogens. Then seeds were soaked in water for 24 hour. After soaking, seeds were sown in trays as per the treatment and submerged water level was maintained for 25 days and then twenty five days old rice seedlings were used for further experiment.

Pot experiment

A total of 48 pots were taken and filled with 10 kg of soil. The recommended dose of 40 kg P_2O_5 ha^{-1} as single super phosphate and potassium @ 40 kg K_2O ha^{-1} as murate of potash (MOP) was applied to all the treatments uniformly as basal. Nitrogen @ 80 kg ha^{-1} was applied in the form of urea at two splits. Fifty percent N as basal and the remaining were at panicle initiation stage. Seedlings were gently removed from trays and transplanted in pot as per the treatments given below and three plants per pot were maintained. All the treatments were maintained separately under three different CO_2 concentration such as ambient, 550 ppm, 700 ppm CO_2 in OTC (Kumar et al., 2017).

Treatment details

T_1- No AMF application

T_2- Application of AMF at the time of transplanting

T_3- Transplanting of mycorrhized seedling

T_4- Mycorrhized seedlings with basal application of AM fungi

All the treatments were replicated five times. Soil and plant samples were collected at regular intervals *i.e.*, 45 days after transplanting (DAT), 60 and 90 DAT for AMF root colonization, sporulation and plant phosphorous uptake.

The soil containing AM fungal spores were isolated by using wet sieving and decanting technique (Gerdemann and Nicolson, 1963). The quantification of AM fungal spores from rhizosphere sample was expressed as number of spores per gram of soil (spore g^{-1} soil). AM fungal colonization in rice roots was assessed by staining the roots with Trypan Blue as described by Phillips and Hayman (1970). The plants were uprooted washed, air dried and subjected for oven drying. The powdered plant samples were digested with tri-acid mixture (HNO_3:$HClO_4$:H_2SO_4) and after digestion the samples were filtered and volume was made up to 100ml with sterilized distilled water. The estimation of total phosphorus in digested plant sample was analysed by following vanado molybdate method (Jackson, 1973)

Statistical analysis

The data were analyzed using Web Agri Stat Package version WASP2.0, and subjected to one way analysis of variance (ANOVA). Treatment difference was evaluated using least significant difference (LSD) at $p \leq 0.05$.

RESULTS AND DISCUSSION

Effect of AM fungi on rice root colonization and spore proliferation at ambient CO_2

AM fungal root colonization and spore proliferation were assessed at 45, 60 and 90 DAT and the results are presented in Tables 1, 2 and 3. The results on AMF colonization and spore proliferation at ambient condition (Table 1) revealed that among four treatments the mycorrhized seedlings along with basal application of AMF (T_4) recorded significantly higher sporulation (520-1200 spores 100^{-1} soil) and root colonization (45.0 - 85.0 %) after 45, 60 and 90 DAT as compared to un inoculated control (T_1) and the treatment which received AMF as only basal application (T_2). The AMF spore production was increased up to 60 DAT and then it gradually decreased in all the treatments. The AMF root colonization and spore population did not have any consistent relation among the treatments. In all the AMF inoculated treatments, there was decreasing trend in root colonization after 60 of transplanting, afterwards it was increased at 90 DAT, but this trend was not

Table 1. Effect of AMF on root colonization and its sporulation in rice crop under ambient CO_2 condition

Treatments	45 DAT		60 DAT		90 DAT	
	AMF spore (no./100g soil)	AMF root colonization (%)	AMF spore (no./100g soil)	AMF root colonization (%)	AMF spore (no./100g soil)	AMF root colonization (%)
T^1	400.0(19.8^b)*	17.5(24.5^b)**	401.2(20.0^c)*	25.0(29.8^b)**	265.0(16.2^c)*	32.5(34.4^c)**
T_2	520.0(22.7^b)	40.0(39.2^a)	880.0(29.6^b)	32.5(34.7^{ab})	320.0(17.7^c)	62.5(52.2^b)
T_3	720.0(26.7^a)	42.5(42.1^a)	920.0(30.3^b)	35.0(36.2^a)	420.0(20.4^b)	75.0(60.1^a)
T_4	760.0(27.5^a)	45.0(42.1^a)	1200.0(34.6^a)	37.5(37.7^a)	520.0(22.7^a)	85.0(67.5^a)

**Values in parentheses are arcsine transformed values, *Values in parentheses are square root transformed values, Means within rows followed by the same letter do not differ significantly at $p \leq 0.05$, DAT - Days after transplanting, AMF - Arbuscular mycorrhizal fungi

observed in uninoculated control. Overall, it was observed that the AMF inoculated treatments (T_2, T_3 and T_4) recorded 57-62% higher root colonization than uninoculated control. Among AMF inoculated treatments, mycorrhized seedlings had 4.0-11% higher root colonization than that of treatment which received AMF during the time of transplanting (T_2) at 45 DAT. Similar type of trends were observed at 60 and 90 DAT. Most of the research findings have clearly proved that application of AM fungi significantly improved mycorrhizal colonization and plant growth (Banerjee et al., 2013; Panneerselvam et al., 2012). Some reports indicated that wetland rice plants in submerged fields were highly colonized (Ilag et al. 1987; Sivaprasad et al., 1990; Secilia and Bagyaraj, 1992) by AMF.

Effect of AM fungi on its root colonization and spore proliferation at elevated CO_2 (550 and 700 ppm) condition

The results on AM fungal root colonization and spore proliferation observed after 45, 60 and 90 DAT presented in Tables 2 and 3. Similar to ambient condition, the AMF spore population was increased upto 60 days and then it decreased in all the treatments. In general, the mycorrhized seedlings or mycorrhized seedlings with basal application of AMF recorded significantly higher spore population and AMF root colonization upto 60 DAT under 550 and 700 ppm CO_2 condition compared to uninoculated control. The AMF inoculated treatments (T_2, T_3 and T_4) recorded 14.2-46.7 % higher root colonization than uninoculated treatment (T_1) at 60 DAT. It was well documented that the photosynthesis of plants grown in elevated CO_2 was 35% higher than ambient CO_2 plants (De Souza et al., 2008). The increased availability of carbohydrates / carbon in roots and its exudates, might have led to increased AMF colonization in rice plants.

It has been reported that mycelial biomass production by *Hebeloma crustuliniforme* in *Pinus sylvestris* (L.) Karst seedlings was significantly greater under elevated CO_2, up to a threefold increase in comparison with ambient CO_2 conditions (Fransson et al., 2005). This suggests that the fungus was able to produce more mycelium as a consequence of increased C availability. For instance, Sanders (1998) showed that at 600 μL L^{-1} of CO_2, the external hyphae of AMF showed an increased growth in the rhizosphere of *Prunella vulgaris* in comparison with ambient CO_2 (350 μL L^{-1}), which can be explained by increased allocation

Table 2. Effect of AMF on root colonization and its sporulation in rice cropunder 550 ppm CO_2 condition

Treatments	45 DAT		60 DAT		90 DAT	
	AMF spore (no./100g soil)	AMF root colonization (%)	AMF spore (no./100g soil)	AMF root colonization (%)	AMF spore (no./100g soil)	AMF root colonization (%)
T_1	400.0(19.8^c)*	20.000(26.5^c)**	408.7(20.2^d)*	25.0(39.8^b)**	270.0(16.4^d)*	42.5(40.6^b)**
T_2	640.0(25.1^b)	35.000(36.2^b)	600.0(24.4^c)	30.0(33^b)	400.0(19.8^c)	87.5(69.5^a)
T_3	800.0(28.2^{ab})	40.000(39.2^{ab})	880.0(29.6^b)	50.0(45^a)	560.0(23.6^b)	45.0(42.11^b)
T_4	880.0(29.6^a)	45.000(42.1^a)	1200.0(34.6$^{a)}$	57.5(49.3^a)	720.0(26.7^a)	47.5(43.5^b)

**Values in parentheses are arcsine transformed values, *Values in parentheses are square root transformed values, Means within rows followed by the same letter do not differ significantly at $p \leq 0.05$, DAT - Days after transplanting, AMF - Arbuscular mycorrhizal fungi

Table 3. Effect of AMF on root colonization and its sporulation in rice cropunder 700 ppm CO_2 condition

Treatments	45 DAT		60 DAT		90 DAT	
	AMF spore (no./100g soil)	AMF root colonization (%)	AMF spore (no./100g soil)	AMF root colonization (%)	AMF spore (no./100g soil)	AMF root colonization (%)
T_1	400.0(19.8^b)*	27.5^c(31.5)**	403.7(20.0^c)*	36.25(36.9^b)**	302.7(17.3^c)*	22.5(28.2^c)**
T_2	490.0(21.9^{ab})	45.0^b(42.1)	840.0(28.9^b)	42.5(40.6^a)	680.0(26.0^a)	27.5(31.3^c)
T_3	680.0(25.9^a)	45.0(42^b)	880.0(29.6^b)	56.2(48.6^a)	720.0(26.9^a)	42.5(40.6^b)
T_4	680.0(25.9^a)	60.0(50.8^a)	1320.0(36.6^a)	67.5(55.2^a)	760.0(27.5^a)	55.0(47.8^a)

**Values in parentheses are arcsine transformed values, *Values in parentheses are square root transformed values, Means within rows followed by the same letter do not differ significantly at $p \leq 0.05$, DAT - Days after transplanting, AMF - Arbuscular mycorrhizal fungi

of C to their external hyphae (Rillig and Allen, 1999). Similarly, internal hyphae of AMF showed the tendency to increase. This might also be due to increased root biomass as a result of increased CO_2 levels (Sanders et al., 1998). The results from the present experiment on rice showed that percentage root colonization by the AM fungi was increased under an elevated atmospheric CO_2 concentration, in line with earlier findings (Rillig et al., 2002; Johnson and Gehring, 2007; Cheng et al., 2012). However, some other studies have reported no responses or even decrease in root AM levels of plants grown under high CO_2 concentrations (Rillig et al., 2002; Cavagnaro et al., 2007). It is proposed that differences in AM fungi, plant species, and duration of the experiment could have brought about these discrepancies.

Effects of AM fungi on plant nutrient uptake under ambient and elevated CO_2 condition

The effect of AMF application on plant P uptake in rice at ambient and elevated CO_2 is presented in table 4. The phosphorous content was analyzed at 45 DAT and maturity stage and results indicated that, at ambient condition there was no significant variation in phosphorous content in plants among different treatments at 45 DAT, but at maturity stage mycorrhized seedlings along with basal application of AMF (T_4) recorded significantly higher plant (0.238 %) and grain (0.289 %) P content compared to other treatments. At 550 ppm CO_2, there was significant variation in phosphorous uptake among various treatments at 45 DAT and maturity stage. However, there was no consistent trend between AMF inoculated and uninoculated treatments. The grain P content (0.288 %) was significantly higher in mycorrhized seedling (T_3) at maturity stage as compared to all other treatments. The results on plant phosphorous uptake at 700 ppm CO_2 revealed that, there was no significant variation in P content in plants among various treatments at 45 DAT, but significant variation was observed at maturity stage of plants. The mycorrhized seedlings along with basal application of AMF recorded significantly higher P content in plants (0.233%) and grains (0.276 %) compared to other treatments.

Many studies have shown that plant growth, P and Zn nutrition of wetland rice were improved under pot culture conditions following inoculation with AM fungi isolated from paddy and non-paddy soils (Sharma et al., 1988; Secilia and Bagyaraj, 1992, 1994). The

Table 4. Effect of AMF on plant phosphorous uptake under ambient elevated CO_2 (550 and 700 ppm) condition.

Treatment	Ambient CO_2			550ppm			700 ppm		
	45 DAT	Maturity stage		45 DAT	Maturity stage		45 DAT	Maturity stage	
	Plant P(%)	Plant P(%)	Grain P(%)	Plant P(%)	Plant P(%)	Grain P(%)	Plant P(%)	Plant P(%)	Grain P(%)
T_1	0.103	0.175^b	0.221^c	0.083^b	0.210^a	0.225^d	0.090	0.170^c	0.225^d
T_2	0.095	0.175^b	0.271^b	0.100^a	0.163^c	0.247^c	0.113	0.165^c	0.254^c
T_3	0.090	0.230^a	0.187^d	0.068^c	0.205^a	0.288^a	0.098	0.180^b	0.262^b
T_4	0.095	0.238^a	0.289^a	0.093^{ab}	0.180^b	0.283^b	0.098	0.233^a	0.276^a
CD ($p \leq 0.05$)	NS	0.01	0.002	0.014	0.016	0.003	NS	0.009	0.007

Means within rows followed by the same letter do not differ significantly at $p \leq 0.05$, DAT - Days after transplanting, AMF - Arbuscular mycorrhizal fungi

beneficial effects of inoculation of crop plants with arbuscular mycorrhizal fungi (AMF) are becoming widely recognized, mainly because these fungi can improve P nutrition under certain conditions (Jeffries, 1987). From this report, it was confirmed that for arbuscular mycorrhizal establishment, inoculation at an earlier stage or at certain interval before flooding was important. The AM fungi can adapt to both low and high levels of soil nutrients. Lambert et al. (1980) who compared the performance of several AM fungi in soils with low levels of extractable phosphorus, found that plant yield was always highest when the inoculum used was indigenous to the soil in which the plants were grown. Similarly, Henkel et al. (1989) reported that adaptation to low P soils occurred within the indigenous AMF population. On the other hand, arbuscular mycorrhizae are often present in soils with high levels of extractable P and these fungi have been considered to be P tolerant (Porter et al., 1978; Sylvia and Schenck, 1983; Douds and Schenck, 1990).

The AMF inoculation increased the P and N concentrations of unhulled grain even though the AM symbiosis became parasitic to wetland rice (Solaiman and Hirata, 1995). Many studies showed that mycorrhizal fungi could enhance the plant uptake of phosphorus (Li et al., 2006; Antunes et al., 2007; Manjunath and Habte, 1988). Mycorrhization of plants with *G. mosseae* caused a significant mobilization of insoluble P in the substrate and uptake by plants. Mycorrhizal plants have increased uptake of P from poorly soluble P sources through either direct or indirect mechanisms deriving from the effects of AMF on rhizosphere properties including changes in pH (Li et al., 2001) and root exudates pattern (Laheurte et al., 1990). Elevated atmospheric CO_2 levels usually enhance the AMF root colonization (Tylianakis et al., 2008) and it can promote plant growth at elevated CO_2 (Kumar et al., 2017) due to the enhanced nutrient uptake and improved photosynthetic rate of the host (Baslam et al., 2012).

CONCLUSION

The present findings clearly indicated that, the crop phosphorous uptake in flooded rice can be improved through application of AMF; however the right method of AMF application is very important rather than merely application. The observation also revealed that, the external application of AMF works better at recommended level of fertilizers in flooded rice cultivation at ambient as well as elevated CO_2 conditions. Among different methods of AMF application, transplanting of mycorrhized seedlings is better in enhancing mycorrhizal colonization and plant phosphorous uptake as compared to the regular method of basal application of AMF.

ACKNOWLEDGEMENTS

The first author thanks to Director, ICAR-National Rice Research Institute, Odisha, India for providing excellent facility for conducting this research work.

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