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Bioprospecting aerobic rice (*Oryza sativa*) and mycorrhizal interaction for nutrient uptake and plant growth

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ABSTRACT

With the growing concern of water scarcity in agriculture, aerobic rice (*Oryza sativa* L.) is a promising mode of cultivation for reducing water use, although the reduced optimal plant growth and yield are major constraints. Arbuscular mycorrhiza (AM) are known to readily colonize rice roots under aerobic conditions, however, the response of upland and lowland rice genotypes has not been investigated. This study was carried out during 2018–19 at ICAR-IARI, New Delhi, using a mycorrhizal consortium and percent colonization was observed to be higher by 58% in upland rice genotypes. AM- upland plants also showed 20% higher plant biomass. AM colonization significantly enhanced rice growth under aerobic conditions, with the upland rice genotypes. Pyari and Satyabhama showed higher response upon AM inoculation. AM colonization increased the total chlorophyll by 54% and the upland rice genotypes showed 51% enhanced nitrogenase activity in their root zones, with highest recorded for Satyabhama. The AM plants showed enhanced activities of nitrate reductase (NR) and glutamine synthetase (GS), and interestingly, the rice genotypes with higher NR and GS (Pyari, Satyabhama) also exhibited more (20%) biomass production and plant N content (36%). Significant varietal differences were recorded in terms of accumulation of antioxidant compounds such as ascorbate, glutathione and proline in AM inoculated plants, which helped to alleviate negative effects of water stress in rice plants under aerobic cultivation.

Keywords: Aerobic rice, Antioxidants, Arbuscular mycorrhiza, Glutamine synthetase, Nitrate reductase

Rice (*Oryza sativa* L.) is extremely sensitive to drought stress therefore grown under continuous submergence. About 75% of the rice is produced by conventional flooding method, and 3000-5000 L of water is needed to produce one kilogram of grain. Since water scarcity has become serious problem, aerobic system has emerged as water-energy-labour saving, highly mechanized, climate adaptable and highly economical system of rice cultivation (Kumar and Ladha 2011). In this system, rice is grown under non-flooded conditions in non-puddled and unsaturated (aerobic) soil using supplementary irrigation. Aerobic rice reduces water use by 27–51% by limiting water loss due to seepage, percolation and evaporation and increase water productivity by 32–88% (Bouman *et al.* 2007). Despite these benefits, reduction in productivity, nutrient deficiency is reported under aerobic systems (Pal *et al.* 2008). The ability of microorganisms in enhancing plant growth under water stress is well documented (Ruiz-Sanchez *et al.* 2010). AM symbiosis increases nutrient and water uptake in plants by external hyphae, regulation of stomatal conductance and increased activity of antioxidant enzymes (Birhane *et al.* 2012, Younesi *et al.* 2013). Under aerobic conditions, rice plants readily form mycorrhizal associations as compared to submerged conditions where anoxic environment limits mycorrhizal infection process. Rice can also be grown with alternate irrigation to reduce water input and creation of aerobic conditions for better AM fungi colonization in rice roots. Therefore, an investigation was undertaken to understand the benefits of AM association for rice plant growth and development under aerobic conditions.

MATERIALS AND METHODS

Experimental setup: The study was carried out during 2018–19 in a pot experiment, in the glasshouse of National Phytotron Facility of ICAR-Indian Agricultural Research Institute (ICAR-IARI), New Delhi, India. This experiment was laid out with three replicates in factorial design, including treatments of eight rice genotypes with/ without mycorrhizal treatment. Eight rice genotypes were selected based on their positive response to mycorrhizal colonization. Four selected rice genotypes are adapted for

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lowland conditions- Pusa Basmati (PB) 1509, PB 1121, Pusa Sugandha 5 (PS 5) and PB 1612; and remaining four were upland varieties- Pyari, Satyabhama, CR Dhan 205 and CR Dhan 202 were selected for the study. Mycorrhizal treatments included inoculation with the consortium of *Glomus intraradices* and *Glomus mosseae* and its sterilized soil counterpart. The consortium of mycorrhizal fungi was procured from Division of Microbiology, ICAR-IARI, New Delhi. Ten seeds of each genotype were sown per pot containing 2 kg sterilized soil with basal application of 100 mg/kg N. In the AMF treatments, inoculum (200 g) was mixed uniformly with the soil. In the non-AMF treatment, an equivalent amount of sterilized soil was added. The plants were thinned to five seedlings per pot after emergence. The pots were watered daily with deionized water, maintaining the soil at a water saturation level. The temperature in the glasshouse was maintained at 30±2°C, 12/12 light/dark period with 60–70% relative humidity.

Sampling and analyses: Plants were harvested at flag leaf stage. Shoots were cut off at ground level and soil was washed from the roots with tap water. Shoots and roots were rinsed in deionized water. Mycorrhizal root colonization was determined as described by Phillips and Haymann (1970). Mycorrhizal responsiveness (MR) was calculated using the formula designed by Hetrick *et al.* (1992).

$$MR = \frac{\text{Plant dry weight}_{+\text{ AMF}} - \text{Plant dry weight}_{-\text{ AMF}}}{\text{Plant dry weight}_{-\text{ AMF}}} \times 100$$

Available N in soil was measured using alkaline permanganate. The shoots and remaining roots were oven dried at 70°C for 48 h, and weighed. Dried and ground plant samples were digested in di-acid mixture ($HNO_3 + HClO_4$) for plant nitrogen (N), phosphorus (P) and potassium (K) analysis. Each root system from these plants was scanned with an EPSON flat-scanner and analyzed with RHIZO 2016a. Chlorophyll content in flag leaves was determined as described by Hiscox and Israelstam (1979). The chlorophyll *a* and *b*, total chlorophyll were computed using formula suggested by Arnon (1949). Dehydrogenase activity of soil samples was estimated by the method described by Casida *et al.* (1964). For measuring nitrogenase activity in soil, gas chromatographic estimation of ethylene in the soil cores placed in tubes was quantified (Prasanna *et al.* 2003). The soil samples were incubated under a gas mixture which had been substituted with 10% acetylene under standard growth conditions for 24 h. Commercially available standard ethylene was utilized for quantification and vials with equivalent volume of water were taken as controls. Glutamine synthetase (GS) activity was determined in the fresh leaves *in vitro* using procedure developed by Mohanty and Fletcher (1980). NR activity in flag leaf was measured by *in-vitro* method of nitrate reductase (NR) assay (Hageman and Reed 1980). Free proline was extracted from 250 mg of fresh leaves (Bligh and Dyer 1959). The methanolic phase was used for quantification of proline content. Proline was estimated by spectrophotometric analysis at 530 nm based on ninhydrin reaction, according to Bates *et al.* (1973). Glutathione content was measured spectrophotometrically at 412 nm, as described by Smith (1985). Ascorbate was assayed photometrically by the reduction of 2,6-dichlorophenolindophenol (DCPIP) as described by Leipner *et al.* (1997). Lipid peroxides were extracted by the method described by Minotti and Aust (1987) and lipid peroxidation was estimated according to

Table 1 Interaction between rice genotypes and AMF inoculation for root parameters[a]

Variety	Root dry weight (g pot^{-1})		Root length (cm)		Root surface area (cm^2)		Root volume (cm^3)	
	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
PB 1509	19.00^{a}	25.33^{abc}	35.10^{a}	40.50^{a}	16.76^{ab}	23.97^{bc}	17.38^{a}	29.91^{bc}
PB 1121	18.91^{a}	21.22^{c}	34.30^{a}	42.20^{a}	16.31^{ab}	22.71^{c}	17.54^{a}	22.34^{d}
PS 5	17.62^{a}	21.27^{c}	34.00^{a}	41.20^{a}	20.57^{a}	20.61^{c}	17.81^{a}	21.02^{d}
PB 1612	18.25^{a}	25.31^{abc}	34.70^{a}	40.80^{a}	13.07^{b}	23.71^{bc}	15.96^{a}	25.53^{cd}
Pyari	18.97^{a}	26.97^{ab}	34.40^{a}	42.40^{a}	14.03^{b}	28.92^{a}	14.23^{a}	31.89^{ab}
Satyabhama	19.84^{a}	30.17^{a}	35.40^{a}	43.90^{a}	15.15^{b}	31.23^{a}	14.59^{a}	36.75^{a}
CR Dhan 205	20.5^{a}	24.31^{bc}	36.10^{a}	41.20^{a}	14.09^{b}	28.65^{a}	15.87^{a}	22.08^{d}
CR Dhan 202	19.66^{a}	22.66^{bc}	35.60^{a}	40.70^{a}	14.40^{b}	27.49^{ab}	15.31^{a}	24.74^{d}
Mean	19.09^{b}	24.65^{a}	34.95^{b}	41.61^{a}	15.55^{b}	25.92^{a}	16.08^{b}	26.78^{a}
Analysis of variance								
Condition	0.00009****		0.00009****		0.00009****		0.00009****	
Variety	0.00073***		0.95780^{ns}		0.00332**		3.7788e-06****	
Condition × Variety	0.01025*		0.94047^{ns}		0.00009****		4.5000e-09****	

*, **, ***, **** F values significant at the P=0.05, P=0.01, P=0.001 and P≤0.0001 levels, respectively. ns means non-significant at the P=0.05 level. [a]Data are average of three replicates. Different letters indicate statistical significance at the P=0.05 level within the same column and same conditions. Condition=with AMF and without AMF.

the method of Halliwell (1989). The data was analyzed statistically by standard analysis of variance (ANOVA) and differences were separated by least significant difference (LSD) using SAS version 9.3 (SAS Institute, Inc., Cary, NC, USA 1990).

RESULTS AND DISCUSSION

Root colonization by AMF was found significantly different (P≤0.05) among the upland genotypes ranging from 27.24–39.84%, and non-significant among lowland genotypes. Average mycorrhizal responsiveness based on plant dry weight of rice genotypes was 63.99% and 45.48% for upland and lowland genotype. The beneficial effects of mycorrhiza on plant growth under drought conditions have been well documented Lee *et al.* (2012). Bernaola *et al.* (2018) reported the natural colonization of AMF in rice plants. Inoculation with mycorrhizal consortium significantly increased the shoot (Fig 2a) and root dry weight (Table 1). There was a significant interaction (P≤0.0001) between varieties and AMF treatments as illustrated by the values of shoot and root dry weights. AM-upland rice genotypes recorded higher shoot (54.9%) and root (29.12%) dry weights. Root parameters were significantly influenced by the AMF inoculation (P≤0.05). Root lengths recorded were statistically at par for all varieties but root surface area and volume affected significantly by 66.68% and 66.54%, respectively upon AMF treatment. The effect was much higher in upland varieties as compared to lowland varieties (Table 1). Wangiyana *et al*. (2018) have shown the increase in total biomass, dry straw and grain yield in AM inoculated rice under aerobic rice.

AMF treatment brought significant difference in the nutrient content (shoot N and P increased by 35.5% and 112.5% respectively) of rice (P≤0.05) (Table 2). The interaction between AMF treatment and rice varieties for shoot N was non-significant. Both upland and lowland varieties, gave a strong response towards mycorrhizal colonization as 95-98% increase in P content was observed as compared to uninoculated counterparts. AMF treatment significantly affected the availability of N in soil (P≤0.0001). Soil available N increased by 10.02% in AM-treated varieties. Varietal effect on N availability in soil was also significant. P and K availability in soil was significantly affected by AMF inoculation (P≤0.0001). There was 33.36% and 13.45% increase in availability of P and K, respectively in soil in AM-rice varieties.

Microbial activity measured in terms of dehydrogenase was increased in AMF treated plants (Fig 1a). Highest dehydrogenase activity was recorded for Satyabhama (15.96 µg TPF/g soil/day). The dehydrogenase activity was positively correlated to the percent colonization which indicates that the presence of AMF together with other soil microflora significantly contributed to increased nutrient status of the AM rice genotypes. AMF inoculation significantly increased the biological nitrogen fixation (BNF) activity in rhizospheric soil as measured by acetylene reduction assay (ARA) (Fig 1 b). The ARA activity was increased by 42.83% and 14.23% in upland and lowland varieties respectively upon AM inoculation. Soil ARA was positively correlated to soil available N and P in both AM and non-AM plants. ARA was positively correlated to mycorrhizal responsiveness (MR). This correlation indicates that genotypes with higher MR may show better free-living nitrogen fixation ability in their root zone, as a result of more availability of soil P.

Analysis of NR and GS activity in flag leaves was undertaken as these enzymes are involved in nitrogen assimilation by plants. NR can be used as stress marker because it is highly sensitive to metabolic and physiological plant status and decreases in leaves exposed to water stress because of lesser flux of nitrate from roots to leaves. Our study helps to correlate NR, plant biomass production

Table 2 Interaction between rice genotypes and AMF inoculation for nutrient status of rice varieties[a]

Rice genotypes	Shoot N (%)		Shoot P (%)		Shoot K (%)		Total chlorophyll in flag leaf (mg/g fresh weight)	
	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
PB 1509	1.32^{a}	1.87^{a}	0.17^{ab}	0.27^{c}	2.28^{a}	2.67^{a}	1.90^{a}	2.20^{a}
PB 1121	1.27^{a}	1.74^{a}	0.18^{ab}	0.32^{bc}	2.24^{a}	2.72^{a}	1.62^{bc}	1.82^{bc}
PS 5	1.49^{a}	1.78^{a}	0.18^{ab}	0.27^{c}	2.30^{a}	2.52^{ab}	1.76^{ab}	1.78^{bc}
PB 1612	1.38^{a}	1.83^{a}	0.20^{a}	0.38^{ab}	1.19^{d}	2.24^{b}	1.65^{abc}	1.79^{bc}
Pyari	1.39^{a}	2.02^{a}	0.16^{ab}	0.32^{bc}	1.95^{ab}	2.64^{a}	1.73^{abc}	2.10^{a}
Satyabhama	1.43^{a}	2.19^{a}	0.21^{a}	0.43^{a}	1.57^{c}	2.78^{a}	1.56^{bc}	1.65^{c}
CR Dhan 205	1.45^{a}	1.98^{a}	0.11^{bc}	0.38^{ab}	1.64^{bc}	2.25^{b}	1.65^{abc}	2.02^{ab}
CR Dhan 202	1.27^{a}	1.60^{a}	0.19^{a}	0.35^{b}	1.98^{ab}	2.52^{ab}	1.48^{c}	1.81^{bc}
Mean	1.38^{b}	1.87^{a}	0.16^{b}	0.34^{a}	1.89^{b}	2.54^{a}	1.67^{b}	1.90^{a}
Analysis of variance								
Condition	0.00009****		0.00009****		0.00009****		0.00009****	
Variety	0.00691**		0.00001****		2.00e-10****		0.00009****	
Condition × Variety	0.15675^{ns}		0.00091****		9.257e-06****		0.03501*	

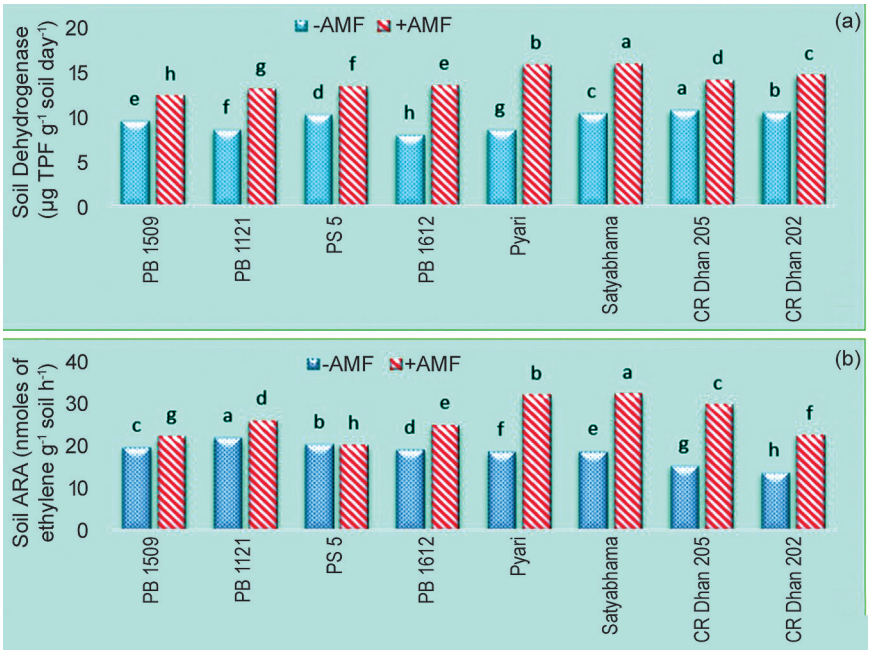

Fig 1 Interactive effect of rice genotypes and AMF inoculation on a) dehydrogenase activity, b) nitrogenase activity in soil.

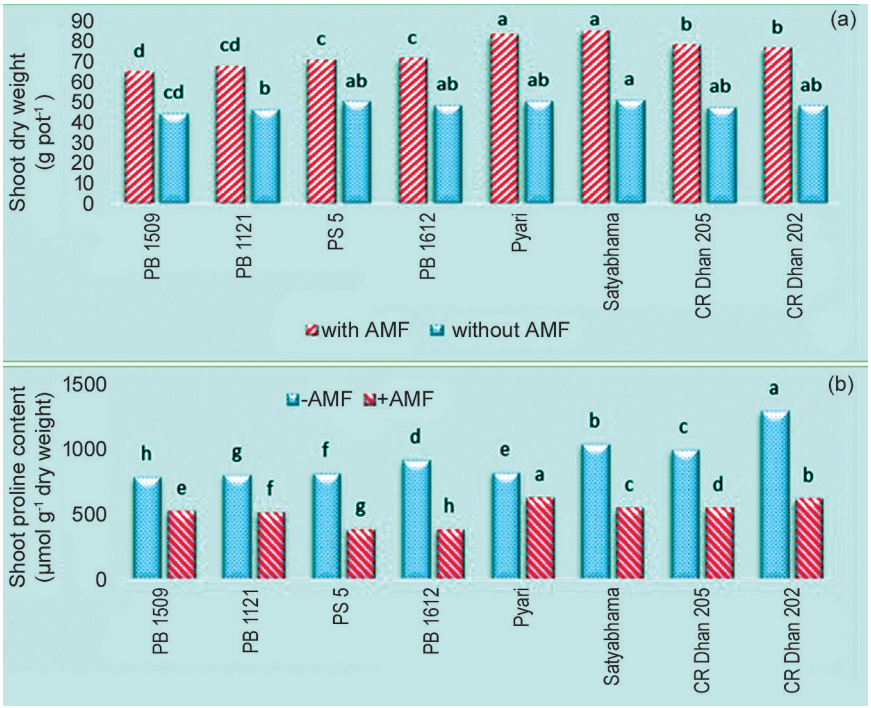

Fig 2 Interactive effect of rice genotypes and AMF inoculation on a) shoot dry weight, b) proline.

and plant N content in rice plants upon AM inoculation. In the same way, NR activity was significantly increased (16.67%) by AM inoculation. The effect was more prominent in upland genotypes indicating strong response to AM colonization. AM-rice varieties displayed 31.86% higher GS activity than uninoculated plants. The higher NR and GS activities in mycorrhizal plants can be related to the phosphate requirements of these enzymes (Hageman and Reed 1980) as mycorrhiza may increase the availability and supply of phosphate to the plant and improve the plant water relations. Similar reports on increase in the NR and GS as a result of better absorption, translocation and assimilation due to AM inoculation have been documented in different crops, including rice (Ruiz-Sanchez *et al.* 2011). AM inoculation significantly increased the chlorophyll content (Table 2). AM upland and lowland rice varieties showed 18.13% and 9.5% higher chlorophyll content, respectively as compared to uninoculated. Higher chlorophyll in AM-colonized plants illustrates better photosynthetic efficiency which can be attributed to the better growth observed in AM-colonized plants. Under water stress conditions, AM-colonized plants show enhanced photosynthetic efficiency and thus increase in shoot biomass (Ruiz-Sanchez *et al.* 2010). Higher chlorophyll produce more photosynthate ensured better substrate availability for the growth and development of root system, AM fungi and rhizospheric microflora (Narwal *et al.* 2018).

The antioxidant accumulation in plants is taken as an index of tolerance to environmental stress. These antioxidant compounds are ascorbate, glutathione, flavonoids, carotenoids and tocopherols. Among these, glutathione and ascorbate are essential metabolites, play important role in antioxidant defense mechanism. Plants under drought stress accumulate proline that protects macromolecules against denaturation. In our study, significant accumulation of proline was observed in the shoots of AM and non-AM rice plants (Fig 2b). The amount of proline accumulated was 78% higher in non-AM plants as compared to AM plants. Among the uninoculated rice varieties, proline content was higher by 24.74% in upland varieties compared to the lowland varieties. The upland-AM rice genotypes showed slightly higher proline accumulation (28%) than lowland-AM rice genotypes. There was a significant interaction between rice genotypes and mycorrhizal inoculation for proline accumulation as evidenced by less accumulation of proline in AM inoculated plants. AM plants may need to accumulate less proline (Ruiz-Sanchez *et al.* 2010) as mycorrhiza helps in improved water uptake to the plant. Pedranzani *et al.* (2016) observed increased

lipid peroxidase, catalase, ascorbate peroxidase activities and lower glutathione reductase and superoxide dismutase activity in the roots of AM inoculated *Digitaria eriantha* cv. Sudafricana plants as compared to uninoculated plants. Overall, AM inoculation increased glutathione content in shoots by 37.5%. Significant difference was noticed in glutathione accumulation between AM-lowland and AM-upland rice genotypes; AM-upland genotypes showed 10% more glutathione content.

Significantly higher (36.8%) ascorbate content was found in AM plants (by 36.8%) than non-AM plants. Difference in ascorbate accumulation was significant among the rice varieties and their interaction with mycorrhizal consortia was also significant. AM-upland rice varieties accumulated 7.99% more ascorbate compared to AM-lowland varieties. The amount of lipid peroxides formed was measured as an index of oxidative damage to lipids as a result of water limiting conditions. The results showed that AM plants contained 70% less lipid peroxides than non-AM plants. The amount of lipid peroxides in AM-upland rice varieties (96.68 nmol MDA/g/ dry weight) was 74.13% lesser than their non-AM counterparts (168.53 nmol MDA/g/ dry weight). Higher chlorophyll content leading to enhanced photosynthesis and hence, less photorespiration may have contributed to less free radical production and hence less damage to membrane lipids in AM plants (He *et al.* 2007).

Correlation analysis: Percent colonization had a significant positive correlation with total chlorophyll (R^2=0.5802), shoot dry weight (R^2=0.7620) and soil dehydrogenase (R^2=0.8502). Percent colonization was positively correlated with soil nitrogenase (R^2=0.4178), but relation was non-significant. Percent colonization seemed to explain 85.02% variability of dependent variable, soil dehydrogenase. AMF colonization had a significant positive correlation with soil available P (R^2=0.5847), but relation with shoot P content was found to be non-significant. Soil dehydrogenase activity had a significant positive correlation with shoot dry weight (R^2=0.9520). Total chlorophyll was positively related with soil dehydrogenase (R^2=0.7990) and soil nitrogenase activity (R^2=0.8390), but the relation with nitrate reductase activity was non-significant.

The findings of the study help to conclude that mycorrhizal colonization can be exploited for the improvement of the growth of rice under aerobic conditions. Continuous cultivation of aerobic rice leads to a decline in productivity with time, but AM symbiosis can alter plant growth by improved root-shoot signaling, enhancing the ability to acquire nutrients and boosting plants to tolerate oxidative damage under aerobic environment. The AM symbiosis helps to improve the photosynthesis under water-limiting conditions. Future studies are warranted to understand whether enhanced nutrient uptake and plant growth at flag leaf stage is translated into high yields.

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