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Effect of Arbuscular mycorrhizal Fungal Colonization on Nutrient Uptake in Rice Aerobic Conditions

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A B S T R A C T

Ten upland rice varieties were grown under aerobic conditions in the fields of IARI, New Delhi and were studied for mycorrhizal status and their growth performance. Rice varieties, Satyabhama and Pyari were shown to have highest response towards mycorrhizal colonization. Percentage of arbuscular mycorrhizal fungi (AMF) root colonization varied between 26.60% and 55.40%. Greater plant nitrogen uptake (110.70 kgha^{-1}) and enhanced biomass (54.9%) were observed with increased AMF colonization. Total Zn and Fe uptake by plants were higher in AMF treated rice by 32.4% and 22.4% compared to untreated control plants, respectively. Zn and Fe uptake was significantly increased by colonization with AMF. Increased biomass of rice plants can be attributed to improved P uptake (19.53 kgha^{-1} - 12.22 kgha^{-1}) due to AM colonization. Mycorrhizal colonization showed positive correlation with the total chlorophyll content and nitrate reductase activity in the AMF treated rice. The study concludes that rice plants grown under aerobic conditions respond strongly to mycorrhizal infection and AM colonization greatly affects the plant nutrient status.

Introduction

About 90% of rice is produced and consumed in Asia, where the demand for rice is on the increase due to increasing population (Bouman, 2001). Rice is a semiaquatic plant and grows well under lowland flooded anaerobic conditions. Irrigated rice is the profligate user of fresh water as it utilizes 24-30% of the world's accessible freshwater resources (Singh, 2013). Toung and Bouman (2003) reported that by the year 2025, about17 million ha (mha) of irrigated rice area in Asia may experience 'physical water scarcity' and 22 mha may face 'economic water scarcity'. Rainfall patterns in many areas are becoming more unreliable, with extremes of drought and flooding occurring regularly. Thus, there is a need to economize water use in irrigated rice production. The transplanted puddled rice production system is labour, water and energy-intensive which proved less profitable (Kumar and Ladha, 2011).

The aerobic rice system (ARS) is a new production system in which rice is grown under non-puddled, non-flooded and non-saturated soil conditions as other upland crops

(Prasad, 2011; Bouman, 2001; Tuong and Bouman, 2003). Thus, in ARS, soils are kept aerobic almost throughout the rice-growing season. The driving force behind ARS is water economy and Castaneda *et al.,* (2003) reported a saving of 73% in land preparation and 56% during crop growth. Yields obtained with ARS varieties vary from 4.5 to 6.5 t/ha, which is 20–30% lesser than that obtained with lowland varieties grown under flooded conditions (Farooq *et al.,* 2009). The yields of aerobic rice gradually decline over time as compared to a continuously flooded control (Peng *et al.,* 2006).

Nishizawa *et al.,* (1971) introduced the term "soil sickness" for the combined effect of allelopathy (Nishio and Kusano, 1975), nutrient depletion (Lin *et al.,* 2002), built-up of soil-borne diseases and pests (Ventura *et al.,* 1981), and soil structure degradation. Thus, yield decline in aerobic rice monoculture over time could be due to both abiotic and biotic stresses.

Currently, there is a growing awareness of the importance of plant microbe interactions in plant performance, particularly for reducing nutrient inputs and minimize the environmental impacts of mineral fertilizers while maintaining plant growth and development (Jez *et al.,* 2016). Soil microorganisms such as AM fungi symbiotically associated with plant roots and interacting with specific microbial communities are able to develop a range of activities to increase plant growth and crop productivity under stressed conditions (Barea *et al.,* 2005; Azcón and Barea, 2010). Beneficial effect of microbial inoculants has been demonstrated in terms of greater biomass production, better nutrient uptake in plants and increase in grain N and P in rice grown under SRI practices (Prasanna *et al.,* 2015) and increased micronutrient uptake (Adak *et al.,* 2016).

Rice plants readily form mycorrhizal associations under upland conditions but, under submerged conditions, infection is rare due to the anoxic environment (Ilag *et al.,* 1987). However, few reports have reported AMF colonization under flooded conditions (Secilia and Bagyaraj, 1994; Solaiman and Hirata, 1996). Thus, to obtain benefits from the AM symbiosis, rice should be grown under non-flooded conditions, creating aerobic conditions in the soil that stimulate colonization of rice roots by AM fungi (Vallino *et al.,* 2009; Ruíz-Sánchez *et al.,* 2010).

Rice can also be grown in a system of alternate irrigation to reduce water input needed for production; this system creates aerobic conditions in the soil that stimulates colonization of rice roots by AM fungi. However, a general view of AM fungal colonization of rice roots under aerobic conditions is not well documented, with a few studies demonstrating the deployment of AM fungi for the benefit of rice plants, under adverse environmental conditions (Vallino *et al.,* 2009). From this perspective, the aim of this study was undertaken with hypotheses (i) AMF colonization in rice plants under aerobic conditions will enhance nutrient mobilization, (ii) AMF symbiosis has significant impact on the yield of rice and (iii) rice varieties differ significantly to the AMF colonization. The overall aim was to determine how this symbiosis influences plant growth, nutrient uptake and photosynthetic performance of rice plants under aerobic conditions.

Materials and Methods

Experimental site and field management

Ten upland rice varieties were grown under aerobic conditions in the fields of IARI, New Delhi. Details of the rice varieties used in the experiment are presented in Table 1. The experiment was conducted at the experimental farm of the ICAR-Indian Agricultural Research Institute (IARI), New Delhi, India (28^o 40' N, 77^o12' E, 228.6 m above the mean sea-level), during the kharif season, 2015. The mean temperature was around 35°C.Of the total recorded rainfall, 18.03, 256.18, 167.29, 19.2 and 2.22 mm were received during the month of June, July, August, September and October, respectively, in year 2015.

The experiment was laid out completely randomized design in three replicates with plot sizes 2 m ×10 m. Plots were separated by bunding. The plots were ploughed twice by disc harrow followed by one ploughing by cultivator, but no puddling was done. Aerobic plots were flash irrigated to keep the soil saturated with water. For sowing seeds, 20 rows were made in each plot, 25cm apart and seeds of all the varieties were drilled at a depth of 2cm. A pre-sowing irrigation was given in the experimental field before sowing of the seed. Recommended doses of N (150kg/ha), P_2O_5 (60kg/ha) and K_2O (50kg/ ha) were applied to crops during the experiment in all the plots. Half dose of N and full doses of P and K were applied basal at the time of sowing and remaining N was applied in 2 equal splits, i.e. at tillering and panicle-initiation stages. The plots were kept weed-free by hand weeding. Irrigations to the crop were provided so as to keep soil near field capacity. Other crop-management practices were followed as per the recommendations. Mycorrhizal treatments included a non-mycorrhizal control and inoculation with the consortia of mycorrhizal fungus *Glomus intraradices* and *Glomus mosseae.* The mycorrhizal consortia was obtained from Division of Microbiology, ICAR-Indian Agricultural Research Institute, New Delhi, India. The inoculums consisted of colonized root segments and attached rhizosphere soil from *Paspalum notatum* were grown in a glasshouse.

Chemical analysis of plant samples

The plant samples from respective treatment plots were collected manually at the time of crop harvest. Ten rice plants were harvested from each plot and separated into grain and straw. Collected plant samples were dried in hot air oven at 60 ± 2 °C for 6 h. The oven-dried samples of plants and air-dried samples of grains were ground to pass through 40-mesh sieves in a macro-Wiley mill and analyzed for N, P, K, Zn and Fe concentrations. Nitrogen, phosphorus and potassium concentrations were analyzed in grain and straw by adopting modified micro-Kjeldahl method for nitrogen, vanado-molybdate yellow colour method for phosphorus and flame photometer method for potassium estimation as described by Jackson (1958). Fe concentration in rice grain or straw was analyzed by EDTA method. The nutrient uptake (kg ha^{-1}) was computed by multiplying nitrogen, phosphorus, potassium and iron concentration with grain or straw yields (kg ha^{-1}).

Chlorophyll content in aerobic rice flag leaves was determined at 30 DAS by the following procedure as depicted by Hiscox and Israelstam (1979). The chlorophyll a and b, total chlorophyll content of leaf was computed using the formula suggested by Arnon (1949). One hundred milligram of leaf tissue was placed in a vial containing 7 ml of DMSO and chlorophyll was extracted in to the fluid by incubating at 65˚C overnight. The extract was then transferred to a graduated tube and made up to a total volume of 10 ml with DMSO, assayed immediately or transferred to vials and stored between 0˚C – 40˚C until required for analysis. Assay was done by transferring 3 ml of chlorophyll extract to a cuvette and the OD values at 645 nm and 663 nm were read in spectrophotometer against a DMSO blank. An *in vitro* method of nitrate reductase (NR) assay (Hageman and Reed, 1980) was used to estimate NR activity in the flag leaves. Crude protein content in rice grain was obtained by multiplying N concentration with a coefficient factor 5.85(Prasad *et al.,* 2006). Mycorrhizal root colonization was determined by the method as described by Phillips and Haymann (1970). Briefly, 1 cm root samples were cleared in 10% KOH, acidified in 2% HCl and stained with 0.05% trypan blue in lactophenol. Fifty root segments (1 cm each) were randomly selected and mounted parallel to each other (ten each on glass slides). Every root segment was observed under microscope (200–400X) and rated according to the range of classes indicated by Trouvelot *et al.,* (1986).

Statistical analysis

The data of all factors 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). For statistical analysis of data, Microsoft-Excel software (Microsoft Corporation, USA) was used and significant differences were determined at LSD ($P \leq 0.05$).

Results and Discussion

Root colonization by AMF

No root colonization by AMF was observed in uninoculated plants. There was a significant variation found in the root colonization among the rice varieties ($P \leq 0.05$). Maximum root colonization with AMF was found at 30 DAS (Fig. 1). Root colonization was decreased by 65% and 120% at 45 and 60 DAS respectively, on an average. Rice variety, Satyabhama showed highest root colonization (55.40%) followed by Pyari (46.07%) at 30 DAS. Root colonization by AMF ranged from 26.60% to 55.40% at 30 DAS, which decreased from 16.07%- 6.00% at 60 DAS.

Nutrient mobilization at flag leaf stage as influenced by AMF treatment

Nutrient concentration in the rice plants was significantly affected by AMF treatment (Table 3). Shoot N concentration was 67.3% higher in AMF treated rice plants as compared to untreated plants. Shoot N content ranged from 1.36% to 2.17%, being highest found in Satyabhama (2.17%) and lowest in DhalaHeera. Shoot P accumulation was significantly at par in untreated control plants.

In AMF treated rice plants, P content was found to be tremendously higher by 101%. Shoot K content was also significantly affected by AMF treatment. There was a difference of about 70.3% in K accumulation in shoot between AMF treated and untreated control plants, being higher recorded in AMF treated rice. Maximum K content was observed in Satyabhama (2.51%) followed by Pyari (2.43%). AMF treatment significantly affected micronutrient accumulation. The Zn and Fe content in shoot were 28.4% and 15.04% higher in AMF treated plants, respectively. Shoot Zn concentration in AMF plants ranged from 36.46 mg kg^{-1} to 57.43 mg kg^{-1}. Highest Fe concentration was found in Satyabhama (159.79 mg kg^{-1}) and lowest in Anjali (31.99 mg kg^{-1}).

Chlorophyll content and Nitrate Reductase (NR) activity as influenced by AMF treatment

A 70.0%, 60.0% and 66.5% higher chlorophyll *a*, chlorophyll *b* and total chlorophyll content respectively was observed in AMF treated rice plants. Total chlorophyll content in AMF rice ranged from 1.64 mg g^{-1} fresh weight to 3.26 mg g^{-1} fresh weight, highest being recorded for Satyabhama. The concentration of different chlorophyll pigments was found to be almost non-significant among control rice plants.

Similarly, NR activity was significantly at par in control rice plants (Table 9). NR activity was found to be significantly higher in AMF treated rice plants. Highest NR among AMF treated rice was recorded for Satyabhama (41.12 µmoles of nitrite formed h^{-1} g^{-1} fresh weight) and CR Dhan204 exhibited lowest NR activity (25.25 µmoles of nitrite formed h^{-1} g^{-1} fresh weight). The interaction between rice varieties and AMF treatment was found to be significant.

Nitrogen (N) concentration and uptake as influenced by AMF treatment

Nitrogen uptake differed significantly ($P \leq 0.05$) between AMF treated and untreated rice (Table 4). Nitrogen concentration in both grain and straw was higher in AMF treated rice by 44.6% and 38.9%, respectively as compared to control rice. AMF treated rice varieties Satyabhama and Pyari were recorded for highest N content in grain (1.87%) and straw (0.62%) respectively. Satyabhama and Pyari were recorded for highest N uptake by grain (74.80%) and straw (44.64%), respectively. Total N uptake was higher in AM colonized rice by 41.8% compared to uninoculated plants. Among the non- AM treatments, Satyabhama showed maximum total N uptake (110.70 kg ha^{-1}) followed by CR Dhan 205 (87.06 kg ha^{-1}). There was a significant interaction between rice varieties and AMF treatment which is evident by the higher N concentration and uptake in AM-rice as compared to non-AM rice.

Phosphorus (P) concentration and uptake as influenced by AMF treatment

Rice variety Satyabhama was recorded for a significantly higher concentration of P in both grain (0.37%) and straw (0.24%) (Table 5). P content in grain was higher by 36.5% in AM treated rice. Similarly, P uptake in grain and straw was higher in AM rice by 37.8% and 31.2% compared to non-AM rice. In control rice plants, 33.8% less total P uptake was observed. Satyabhama was recorded for highest P uptake in grain (12.80 kg ha^{-1}) and straw (16.80 kg ha^{-1}). The P concentration in grain and straw and its uptake was more or less at par in non- AM rice. The interactive effect of rice varieties with AMF shows that all the rice varieties accumulated higher P in grain and straw and their total when AM colonized.

Potassium (K) concentration and uptake as influenced by AMF treatment

K concentration in grain was found to be non-significant among rice varieties whether AM colonized or not (Table 6), although K concentration in grain was higher in AM rice by 31.5% compared to non-AM rice. K concentration in straw was significantly at par among uninoculated plants. In AM colonized rice, Dhala Heera exhibited highest K accumulation (1.62%) in straw. K uptake by grain in AM-rice ranged from 13.30 kg $ha^{-1}$to 20.00 kg ha^{-1} and this was 30.9% higher compared to non-AM rice. Total K uptake was significantly higher in AM-rice by 11.2%. The interactive effect of rice varieties and AMF treatment was non-significant which is evident by the results that CR Dhan 205, CR Dhan 202 and Satyabhama did not show increase in total K uptake upon AMF treatment.

Zinc (Zn) concentration and uptake as influenced by AMF treatment

Zn concentration in grain and straw and its uptake was significantly affected upon AMF treatment (Table 7). Zn concentration in AM treated rice ranged from 26.44 mg $kg^{-1}$to 53.64 mg kg^{-1}, this was higher by 32.4% compared to untreated rice. Maximum Zn accumulation was recorded for Satyabhama (72.7 mg kg^{-1}) upon AMF colonization but in control plants, Pyari accumulated almost similar Zn content

(71.2 mg kg^{-1}). Zn uptake by grain was 31.5% higher in AMF treated rice plants. Satyabhama was recorded for highest Zn uptake in grain (214.56 g ha^{-1}), in straw (508.9 g ha^{-1}) and their total (723.46 g ha^{-1}). A difference of only 10.8% was noted for total Zn uptake between AMF treated and control rice plants. The interaction between rice varieties and AMF treatment was found to be non-significant which is clear from the observation that seven out of ten rice varieties did not show increase in Zn concentration and uptake in straw. But the interaction was significant for Zn content in grain and straw and total Zn uptake.

Iron (Fe) concentration and uptake as influenced by AMF treatment

Fe concentration in grain and straw was 24.6% and 22.1% higher in AMF treated rice (Table 8). Maximum Fe concentration in grain was recorded for Anjali (59.09 mg kg^{-1}) and lowest being for Vandana (36.8 mg kg^{-1}) after AMF treatment. The highest Fe accumulation in straw was exhibited by Satyabhama (354.79 mg kg^{-1}). The total Fe uptake in AMF treated rice plants ranged from 1584.63 g ha^{-1}to 2697.93 g ha^{-1} which is almost 22.4% higher compared to untreated plants. The interactive effect of AMF and rice varieties was significant as all the rice varieties showed enhanced Fe content in grain and straw and its uptake by grain and straw and their total.

Shoot dry weight and protein content in grain as influenced by AMF treatment

Treatment with AMF significantly increased shoot dry weight of all the rice varieties under aerobic condition indicating a significant interaction between rice varieties and AMF treatment (Fig. 3). At 30 DAS, shoot dry weight was significantly higher in AMF treated by 57.5% compared to untreated control plants. A 54.9% higher shoot dry weight was recorded for AMF treated rice plants compared to untreated control rice. Shoot dry weight among the AMF treated rice varieties ranged from 35.30 g m^{-2}to 88.67 g m^{-2}, being highest recorded for Satyabhama. AMF inoculation leads to45% increase in protein content in grain (Fig. 4). Satyabhama had accumulated significantly higher protein content (11.13%) over other rice varieties. Protein content among AMF treated rice ranged from 6.96% to 11.13%. Lowest protein concentration was found in CR Dhan 201 (3.93%) in control state.

Correlation analyses

Because maximum colonization of rice roots was observed at 30 DAS, we correlated percent colonization at 30 DAS and the plant parameters (Fig. 2). Non-significant positive correlation was exhibited by rice N and K uptake and percent colonization (R^2=0.32, P= 0.087 and R^2=0.11, P= 0.336). The R^2 value for total P uptake and percent colonization was 0.755, which depicts 75.5% variation in total P uptake of rice as explained by the fitted regression line. On the other hand, the R^2 value for total Zn and Fe uptake indicated 56.2% and 57.9% variability as explained by AMF treatment respectively.

Shoot dry weight was found to be significantly and positively correlated with percent colonization (R^2= 0.64, P=0.005). Regression analysis of total chlorophyll content and NR activity in AMF treated rice and percent colonization reveals 76.5% and 74.7% variability in total chlorophyll content and NR activity depicted by AMF treatment (Fig. 5). Aerobic rice is grown under non-puddled, non-flooded and non-saturated soil conditions (Bouman, 2001; Tuong and Bouman, 2003). The yield of rice under aerobic conditions heavily relies on the adequate supply of plant nutrients including N, P, K, Fe, Zn and others that may become deficient under aerobic conditions.

Table.1 Characteristics of various rice genotypes used in the study

S. No.	Genotypes	Adaptation	Duration (days)	Yield (t/ha)	Areas of adaptability
1.	Vandana	Upland	90-95	3.5	Bihar, Jharkhand and Odisha
2.	CR Dhan 205	Upland	110-115	4.2	Tamilnadu, Odisha, Madhya Pradesh and Punjab
3.	CR Dhan 202	Upland	110-115	3.7	Jharkhand and Odisha
4.	Heera	Upland	70-80	3.0	Jharkhand and Odisha
5.	Anjali	Upland	90-100	3.5	Bihar, Jharkhand and Odisha
6.	CR Dhan 201	Upland	110-115	3.8	Bihar and Chattisgarh
7.	Pyari	Upland	115-120	4.2	Bihar, Jharkhand and Odisha
8.	Satyabhama	Upland	90-110	4.0	Bihar, Jharkhand and Odisha
9.	DhalaHeera	Upland	75-80	3.5	Bihar, Jharkhand and Odisha
10.	CR Dhan 204	Upland	100-110	4.0	Jharkhand and Odisha

Table.2 Physical and chemical characteristics of initial soil samples

Features	Range
1. Physical characteristics	
Sand (%)	52.31
Silt (%)	25.25
Clay (%)	25.49
2. Chemical Characteristics	
Soil organic carbon (%)	0.66
Soil Available N (kg N ha^{-1})	148.35
Soil Available P (kg P ha^{-1})	19.43
Soil Available K (kg K ha^{-1})	239.53
Soil Fe (mgkg^{-1})	11.52
Soil Zn (mgkg^{-1})	3.26
Soil pH (pHTestr 30 pH metre)	7.4
Soil EC(ECTestr 11+)(mS/cm^{2})	973

Table.3 Interactive effect of rice varieties and AM colonization on nutrient concentration at flag leaf stage in rice[a]

	Shoot N (%)		Shoot P (%)		Shoot K (%)		Shoot Zn (mg kg^{-1})		Shoot Fe (mg kg^{-1})	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	1.23cd	1.77ab	0.09c	0.15bc	1.01d	1.56bc	26.38d	36.46cd	43.42def	53.65de
CR Dhan 205	1.01d	1.53bc	0.11c	0.23ab	0.99d	2.03ab	30.52cd	40.6bcd	33.82ef	44.05def
CR Dhan 202	0.99d	1.64abc	0.10c	0.24ab	1.31cd	1.35cd	39.15bcd	49.23abc	45.49def	55.72de
Heera	1.23cd	2.11a	0.11c	0.21ab	1.11d	1.52bc	36.42cd	46.5abc	33.29ef	43.52def
Anjali	1.01d	1.85ab	0.07c	0.16bc	1.26cd	2.11ab	42.58bcd	52.66ab	21.76f	31.99ef
CR Dhan 201	0.97d	1.54bc	0.11c	0.15bc	1.03d	2.31ab	29.25	39.33bcd	84.29cd	94.52c
Pyari	1.05d	2.11a	0.09c	0.27ab	1.05d	2.43a	38.58bcd	48.66abc	62.02de	72.25d
Satyabhama	1.16d	2.17a	0.08c	0.30a	1.13d	2.51a	47.35abc	57.43a	149.56ab	159.79a
DhalaHeera	0.89d	1.36bcd	0.12c	0.26ab	1.09d	1.56bc	29.28d	39.36bcd	84.82cd	95.05c
CR Dhan 204	1.12d	1.75ab	0.09c	0.19abc	1.06d	1.43bcd	35.32cd	45.4bcd	121.62bc	131.85b
Analysis of Variance										
Variety		0.0021***		0.0005***		0.0126*		0.0069**		0.0012***
Variety ×AMF		0.0121*		0.0021**		0.0210*		0.1002^{ns}		0.0121*

*, **, ***, **** 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 of cultivation.

Table.4 Interactive effect of rice varieties and AM colonization on N concentration and uptake in rice[a]

	N concentration in grain (%)		N concentration in straw (%)		N uptake by grain ($kgha^{-1}$)		N uptake by straw ($kgha^{-1}$)		Total N uptake ($kgha^{-1}$)	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	1.30bc	1.61abc	0.41bc	0.54abc	45.50cd	56.35bc	26.65bcd	35.10bc	72.15bcd	91.45ab
CR Dhan 205	1.25bc	1.76ab	0.48bc	0.55abc	52.50bcd	73.92ab	34.56bc	39.60bc	87.06bc	113.52a
CR Dhan 202	1.16c	1.34bc	0.39bcd	0.59abc	42.92cd	49.58bcd	26.13bcd	39.53bc	69.05bcd	89.11bc
Heera	1.22bc	1.73ab	0.44bc	0.59abc	36.60cde	51.90bcd	26.40bcd	35.40bc	63.00cd	87.30bc
Anjali	0.80cd	1.66abc	0.24cd	0.59abc	28.00de	58.10bc	15.60cd	38.35bc	43.60cde	96.45ab
CR Dhan 201	0.66cd	1.17c	0.35bcd	0.61ab	25.08de	44.46cd	23.80bcd	41.48ab	48.88cde	85.94bc
Pyari	1.17bc	1.75ab	0.46bc	0.62a	49.14bcd	73.50ab	33.12bc	44.64a	82.26bc	118.14a
Satyabhama	1.70ab	1.87a	0.61ab	0.61ab	68.00ab	74.80a	42.70ab	42.70ab	110.70a	117.50a
DhalaHeera	0.93cd	1.68abc	0.45bc	0.60ab	32.55cde	58.80bc	29.25bcd	39.00bc	61.80cd	97.80ab
CR Dhan 204	0.77cd	1.28bc	0.35bcd	0.51abc	30.80cde	51.20bcd	24.50bcd	35.70bc	55.30cd	86.90bc
Analysis of Variance										
Variety		0.0121**		0.6301[ns]		0.0326*		0.0169**		0.0012***
Variety ×AMF		0.0421*		0.5023[ns]		0.0310*		0.1102[ns]		0.0121**

*, **, ***, **** 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 of cultivation.

Table.5 Interactive effect of rice varieties and AM colonization on P concentration and uptake in rice[a]

	P concentration in grain (%)		P concentration in straw (%)		P uptake by grain (kgha^{-1})		P uptake by straw (kgha^{-1})		Total P uptake (kgha-1)	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	0.16bcd	0.19bcd	0.14b	0.19ab	5.60cd	6.65cd	9.10bc	12.35abc	14.70c	19.00bc
CR Dhan 205	0.18bcd	0.21bc	0.09c	0.14b	7.56bcd	8.82bc	6.48c	10.08bc	14.04c	18.90bc
CR Dhan 202	0.15cd	0.22bc	0.13b	0.18ab	5.55cd	8.14bc	8.71bc	12.06abc	14.26c	20.20abc
Heera	0.17bcd	0.17bcd	0.14b	0.19ab	5.10cd	5.10cd	8.40bc	11.40abc	13.50c	16.50bc
Anjali	0.16cd	0.22bc	0.15b	0.20a	5.60cd	7.70bcd	9.75bc	13.00abc	15.35bc	20.70abc
CR Dhan 201	0.17bcd	0.24bc	0.18ab	0.23a	6.46cd	9.12abc	12.24abc	15.64ab	18.70bc	24.76ab
Pyari	0.16cd	0.25bc	0.12bc	0.17ab	6.72cd	10.50ab	8.64bc	12.24abc	15.36bc	22.74ab
Satyabhama	0.21bc	0.32a	0.19ab	0.24a	8.40bc	12.80a	13.30abc	16.80a	21.70abc	29.60a
DhalaHeera	0.19bcd	0.22bc	0.14b	0.19ab	6.65cd	7.70bcd	9.10bc	12.35abc	15.75bc	20.05abc
CR Dhan 204	0.15cd	0.28ab	0.16ab	0.16ab	6.00cd	11.20ab	11.20abc	11.20abc	17.20bc	22.40ab
Analysis of Variance										
Variety		0.0123***		0.0001****		0.0291*		0.2131^{ns}		0.0251*
Variety ×AMF		0.0012**		0.0081**		0.0010***		0.0351*		0.0023**

*, **, ***, **** 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 of cultivation.

Table.6 Interactive effect of rice varieties and AM colonization on K concentration and uptake in rice[a]

	K concentration in grain (%)		K concentration in straw (%)		K uptake by grain ($kgha^{-1}$)		K uptake by straw ($kgha^{-1}$)		Total K uptake ($kgha^{-1}$)	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	0.35a	0.38a	1.18bc	1.49ab	12.25bc	13.30bc	76.70bc	96.85ab	88.95bc	110.15abc
CR Dhan 205	0.32a	0.43a	1.20bc	0.96bc	13.44bc	18.06ab	86.40abc	69.12bc	99.84abc	87.18bc
CR Dhan 202	0.35a	0.47a	0.93bc	0.79bc	12.95bc	17.39abc	62.31bc	52.93c	75.26c	70.32c
Heera	0.38a	0.47a	0.94bc	1.12bc	11.40bc	14.10bc	56.40c	67.20bc	67.80c	81.3bc
Anjali	0.27ab	0.51a	1.17bc	1.60ab	9.45c	17.85abc	76.05bc	104.00a	85.50bc	121.85ab
CR Dhan 201	0.29ab	0.49a	1.29bc	1.53ab	11.02bc	18.62ab	87.72abc	104.04a	98.74abc	122.66ab
Pyari	0.39a	0.46a	1.17bc	1.39abc	16.38abc	19.32ab	84.24abc	100.08a	100.62	119.4abc
Satyabhama	0.53a	0.55a	1.58ab	1.39abc	21.20ab	22.00a	110.60a	97.30ab	131.80a	119.3abc
DhalaHeera	0.33a	0.52a	1.15bc	1.62a	11.55bc	18.20ab	107.25a	107.25a	118.80abc	125.45ab
CR Dhan 204	0.37a	0.43a	1.28bc	1.51ab	14.80bc	17.20abc	89.60abc	105.70a	104.40abc	122.9ab
Analysis of Variance										
Variety		0.1352[ns]		0.0014**		0.0051**		0.0151*		0.0211*
Variety ×AMF		0.4251[ns]		0.0123*		0.0211*		0.0032*		0.1238[ns]

*, **, ***, **** 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 of cultivation.

Table.7 Interactive effect of rice varieties and AM colonization on Zn concentration and uptake in rice[a]

	Zn concentration in grain ($mgkg^{-1}$)		Zn concentration in straw ($mgkg^{-1}$)		Zn uptake by grain (gha^{-1})		Zn uptake by straw (gha^{-1})		Total Zn uptake (gha^{-1})	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	33.60bcd	34.11bcd	48.77c	51.73bc	117.60cd	119.38cd	317.01d	336.24d	434.61d	455.63d
CR Dhan 205	19.27cd	26.44cd	55.30bc	55.87bc	80.93d	111.05cd	398.16cd	402.26bcd	479.09d	513.31cd
CR Dhan 202	35.20bcd	49.04abc	63.77ab	64.50ab	130.24bcd	181.45ab	427.25bc	432.15bc	557.49bcd	613.59bc
Heera	26.60cd	49.51abc	60.60abc	61.77abc	79.80d	148.53bc	363.60cd	370.62cd	443.40d	519.15cd
Anjali	39.40bc	53.24a	67.63ab	67.93ab	137.90bc	186.34ab	439.59bc	441.54b	577.49bcd	627.88b
CR Dhan 201	38.13bc	38.64bc	52.47bc	54.60bc	144.89bc	146.83bc	356.79cd	371.28cd	501.69cd	518.11cd
Pyari	26.07cd	26.58cd	71.20a	63.93abc	109.49cd	111.64cd	460.29b	512.64a	622.13b	571.93bcd
Satyabhama	52.40ab	53.64a	62.47abc	72.70a	209.60ab	214.56a	437.29bc	508.90a	646.89b	723.46a
DhalaHeera	33.20bcd	47.04abc	54.00bc	54.63bc	116.20cd	164.64abc	351.00cd	355.09cd	467.20d	519.73cd
CR Dhan 204	19.87cd	50.44ab	60.20abc	60.67abc	79.48d	201.76ab	421.40bc	424.69bc	500.88cd	626.45b
Analysis of Variance										
Variety		0.0022**		0.0321*		0.0035**		0.0029**		0.0215*
Variety ×AMF		0.0231*		0.3351^{ns}		0.0012**		0.2351^{ns}		0.2211^{ns}

*, **, ***, **** 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 of cultivation.

Table.8 Interactive effect of rice varieties and AM colonization on Fe concentration and uptake in rice[a]

	Fe concentration in grain ($mgkg^{-1}$)		Fe concentration in straw ($mgkg^{-1}$)		Fe uptake by grain (gha^{-1})		Fe uptake by straw (gha^{-1})		Total Fe uptake (gha^{-1})	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	13.59d	36.80cd	148.33d	248.65cd	47.56d	128.80cd	964.14e	1616.22cde	1011.71e	1745.02cd
CR Dhan 205	54.55ab	54.42ab	148.33d	239.05cd	229.11a	228.56a	1067.97e	1721.16bcd	1297.08e	1949.72bcd
CR Dhan 202	20.64d	47.19bcd	250.40bcd	250.72bcd	76.36d	174.61bc	1677.68cd	1679.82cd	1754.05cd	1854.43bcd
Heera	51.30abc	51.17abc	143.20d	238.52cd	153.90bcd	153.51bcd	859.20e	1431.12de	1013.10e	1584.63cde
Anjali	55.89ab	59.09a	226.67cd	226.99cd	195.61abc	206.81ab	1473.35de	1475.43de	1668.97cde	1682.25cde
CR Dhan 201	40.09cd	46.62bcd	269.20bcd	289.52bc	152.34bcd	177.15bc	1830.56bc	1968.73abc	1982.90bcd	2145.89bc
Pyari	23.37d	49.91bc	200.27cd	267.25bcd	98.15d	209.62ab	1441.94de	1924.20abc	1540.09cde	2133.82bc
Satyabhama	43.73cd	53.60ab	293.20bc	354.79a	174.92bc	214.41ab	2052.40ab	2483.53a	2227.32b	2697.93a
DhalaHeera	48.88bcd	55.41ab	289.73bc	290.05bc	171.08bc	193.93abc	1883.24bc	1885.32bc	2054.32bc	2079.26bc
CR Dhan 204	47.92bcd	44.46cd	268.27bcd	326.85ab	191.68abc	177.84bc	1877.89bc	2287.95a	2069.57bc	2465.79b
Analysis of Variance										
Variety		0.0008***		0.0054**		0.0008***		0.0043**		0.0212*
Variety ×AMF		0.0023**		0.2190^{ns}		0.0012**		0.1320^{ns}		0.2135^{ns}

*, **, ***, **** 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 of cultivation.

Table.9 Interactive effect of rice varieties and AM colonization on chlorophyll content and NR activity of rice[a]

	Chlorophyll a (mg g^{-1} fresh weight)		Chlorophyll b (mg g^{-1} fresh weight)		Total chlorophyll (mg g^{-1} fresh weight)		Nitrate reductase (µmoles of nitrite formed h^{-1} g^{-1} fresh weight)	
Varieties	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF	-AMF	+AMF
Vandana	0.77d	1.01cd	0.41cd	0.62bc	1.18e	1.64c	15.73d	31.70bc
CR Dhan 205	0.73d	1.80b	0.33d	0.58bcd	1.06e	2.38ab	14.42d	33.00bc
CR Dhan 202	0.81d	1.41c	0.55bcd	0.66bc	1.36de	2.07b	14.44d	32.92bc
Heera	0.72d	1.08cd	0.52bcd	0.57bcd	1.24e	1.66c	15.05d	25.80cd
Anjali	0.83d	1.34c	0.42cd	0.68bc	1.25e	2.02b	14.67d	30.89bcd
CR Dhan 201	0.84d	1.24c	0.45cd	0.69bc	1.29e	1.93bc	14.33d	35.55b
Pyari	0.90d	1.17cd	0.42cd	0.75a	1.32de	1.92bc	14.59d	33.14bc
Satyabhama	1.03cd	2.38a	0.42cd	0.88a	1.45d	3.26a	14.58d	41.12a
DhalaHeera	0.84d	1.34c	0.38cd	0.69bc	1.22e	2.03b	14.73d	33.09bc
CR Dhan 204	0.82d	1.29c	0.35d	0.67bc	1.17e	1.96bc	16.40d	25.25cd
Analysis of Variance								
Variety		0.0125*		0.0014**		0.0289*	**	0.0024**
Variety ×Condition		0.0015**		0.2561^{ns}		0.0029**	ns	0.0003***

*, **, ***, **** 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 of cultivation.

Fig.1 Percent colonization in rice varieties at 30, 45 and 60 DAS

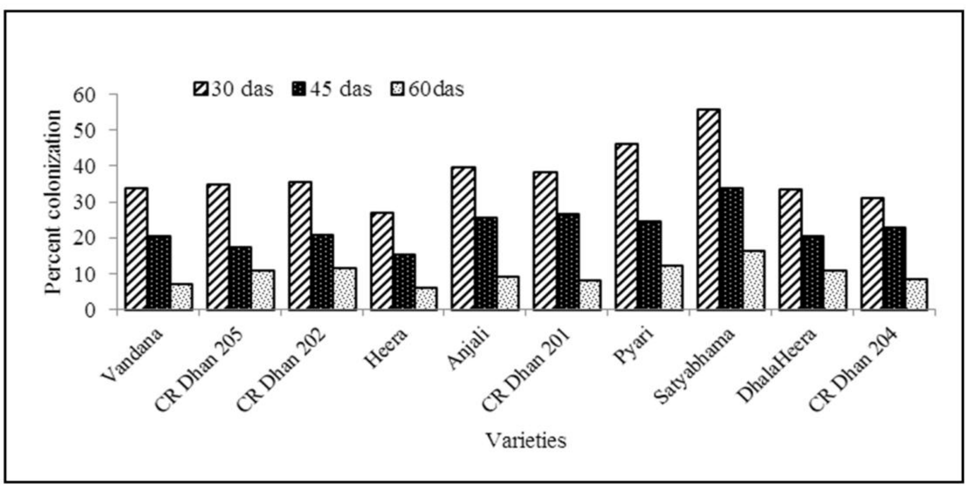


Fig.2 Correlation analyses of percent colonization with A. Total N uptake, B. Total P uptake, C. Total K uptake, D. Total Zn uptake and E. Total Fe uptake of rice plants

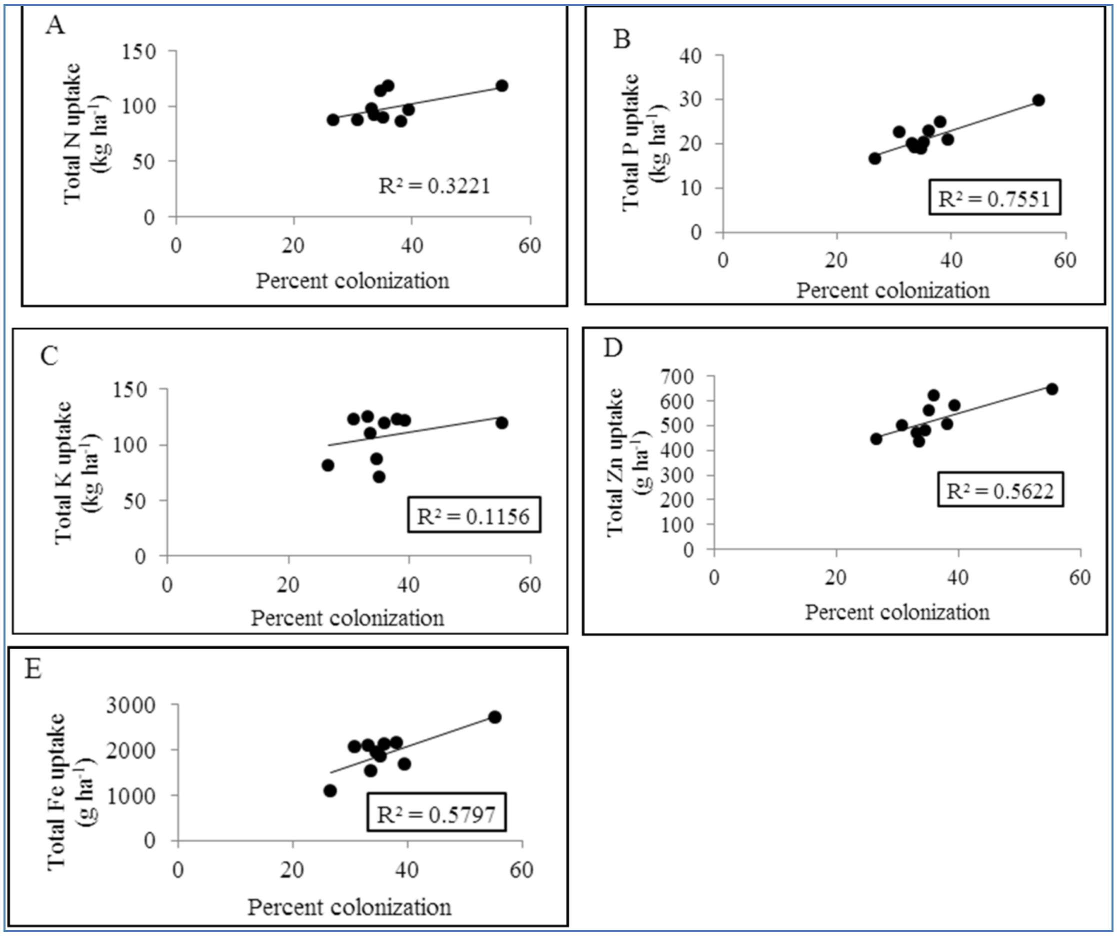


Fig.3 Shoot dry weight as recorded on 30DAS and at the time of harvest

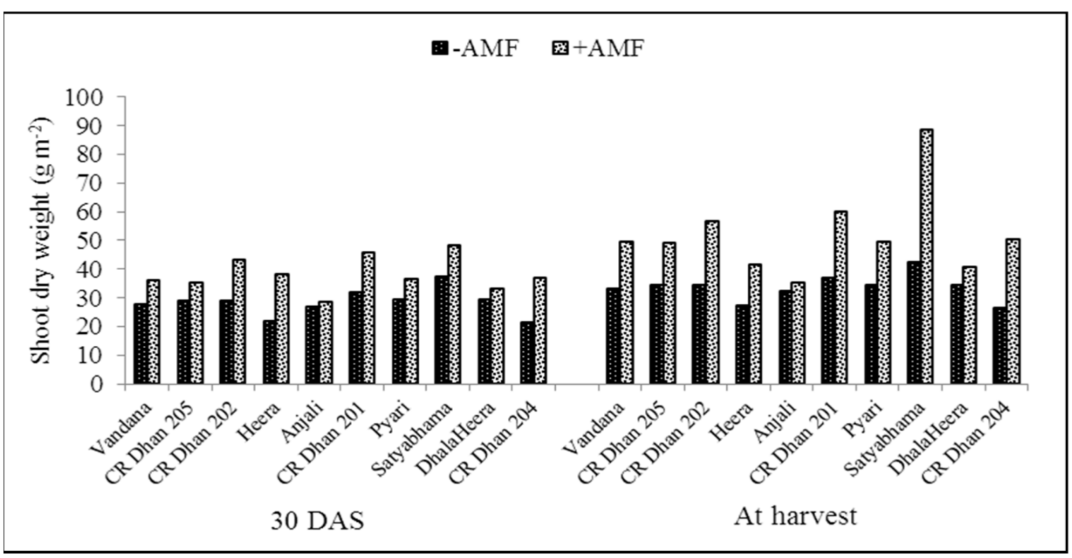


Fig.4 Protein content in grains at the time of harvest of rice varieties

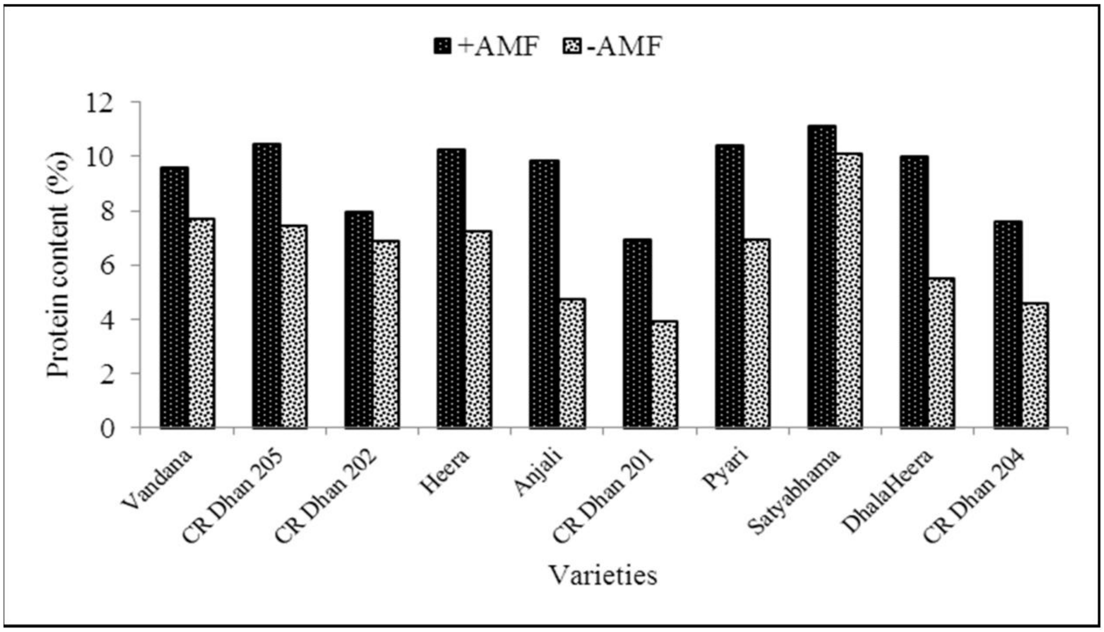
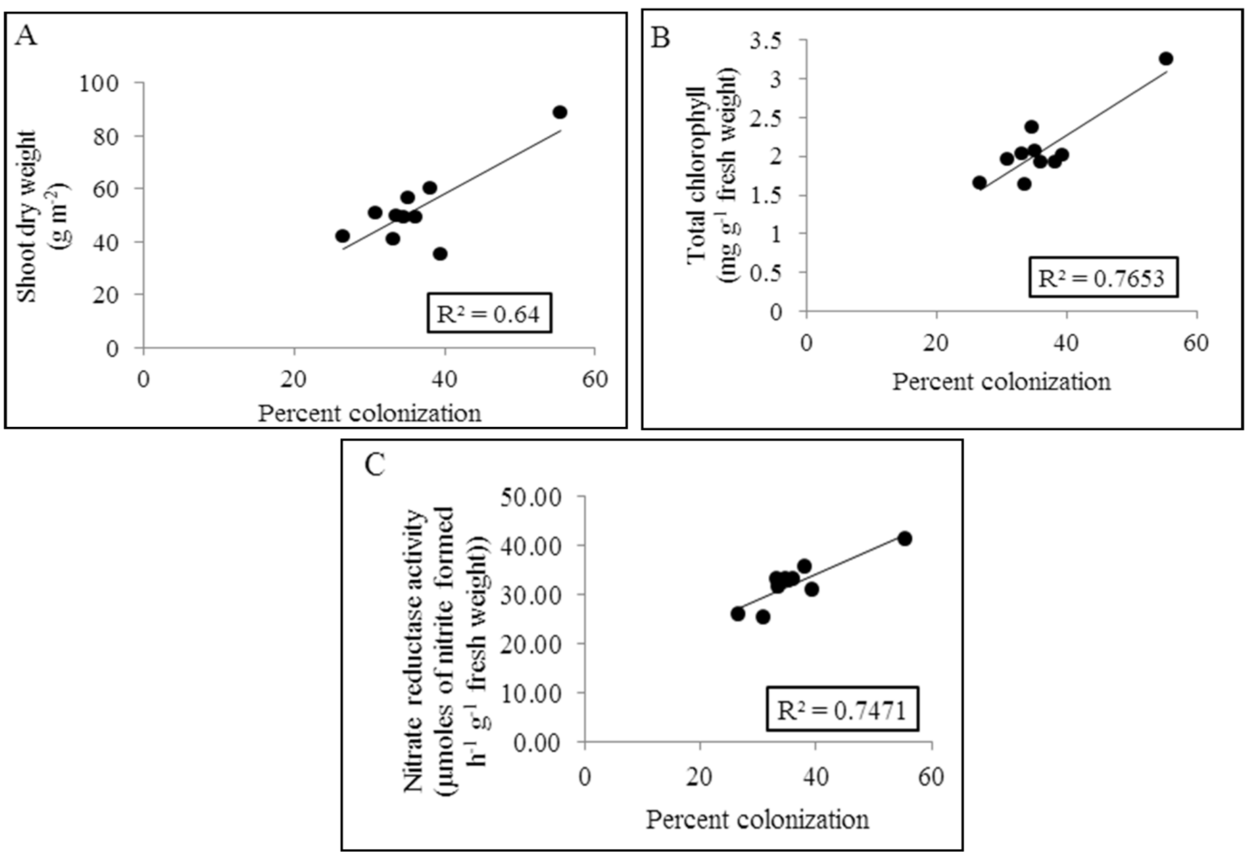


Fig.5 Correlation analyses of percent colonization with A. Shoot dry weight, B. Total chlorophyll content, and C. NR activity of rice plants



Yields obtained with ARS varieties vary from 3.5 to 6.5 t/ha, which is about 20–30% lesser than that obtained with lowland varieties grown under flooded conditions (Farooq *et al.,* 2009). Mycorrhizal symbioses are mutualistic interactions between the root systems of around 80% of land plants and the mycelium of various fungi (Wang and Qiu, 2006). Mycorrhizal fungi participate actively to plant development (Smith and Read, 2008) by improvement of access to nutrients, particularly when resources become scarce. In our study, we demonstrated the potential effect of AMF colonization of rice roots in the earlier growth stage on the nutrient uptake in grain and straw of rice varieties grown under aerobic conditions. We also demonstrated the positive effect of AMF treatment on the total chlorophyll content and NR activity at flag leaf stage of rice varieties.

Maximum root colonization was observed at 30 DAS. According to Miller (2000), during the early phase of the crop cycle, when roots are not yet well developed, AM symbiosis can make an important contribution to plant growth by enhancing nutrient acquisition. Two rice varieties, Satyabhama and Pyari, were highly responsive towards AMF treatment showing maximum root colonization by AMF over other rice varieties at 30, 45 and 60 DAS. All the rice varieties differed significantly with respect to nitrogen (N), phosphorus (P), potassium (K), zinc (Zn) and iron (Fe) concentration in the grain and straw and also their uptake in grain or straw or their total.

Nitrogen concentration in grain and straw and its uptake in grain, straw and their total was found to be significantly higher in AMF treated rice. The positive involvement of AMF in enhanced nitrogen uptake and assimilation by host plant is well documented (Cavagnaro *et al.,* 2012; Lee *et al.,* 2012). Hawkins *et al.,* (2000) reported that AM fungi are able to absorb glycine and glutamic acid and transport nitrogen from these sources to the host plants.

Phosphorus concentration in grain and straw was found to be significantly higher in AMF treated rice plants compared to the control plants. As a result of AMF treatment, P uptake was significantly increased in grain, straw and their total. P plays a very important role in photosynthesis; P is crucial for activation of ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) and in providing phosphorylated intermediates of Calvin cycle (Hernández and Munné-Bosch, 2015).

Similarly, K accumulation was recorded higher in AMF treated rice. A higher level of K accumulation in plants inoculated with AM fungi is well reported in different crops (Borah and Phukan, 2006; Rajesh *et al.,* 2011: Baslam *et al.,* 2013). Maintaining an elevated level of K in plant cells is important for running physiological process like plasma membrane polarization, growth, stomatal aperture or adaptation to adaptation to environmental changes (Anschütz *et al.,* 2014; Shabala and Pottosin, 2014; Benito *et al.,* 2014) and for improvement in hydric stress tolerance (Wu and Xia 2006; El-Mesbahi *et al.,* 2012). These results indicate that AM fungi enhance growth and stress tolerance in rice under aerobic conditions which is accompanied by intermittent drying periods that can be harmful for the growth of rice plants. A significant correlation between K and P during AM symbiosis has been reported by Olsson *et al.,* (2011); results obtained in our study upholds this correlation since rice plants inoculated with AMF displayed significantly higher P and K content as compared to the uninoculated rice plants. Gao *et al.,* (2007) studied the effect of AMF inoculation on growth performance and Zn uptake by rice genotypes varying in Zn uptake when non mycorrhizal and showed that AMF inoculated plants produced more biomass and took up more Zn than non-mycorrhizal controls.

Saia *et al.,* (2014) reported higher biomass production under water stressed conditions in Berseem, clover on AM symbiosis. Increased biomass may be attributed to the enhancement of nutrient uptake offered by AM fungi during active growth stage under aerobic conditions, which satisfied both rice and fungal nutritional needs for growth.

The interaction between the AMF treatment and rice varieties shows that AMF significantly contributed towards nutrient concentration and uptake in rice plants under aerobic conditions. This is also evident by the observation that Satyabhama and Pyari which were recorded for higher root colonization were also reported to have maximum nutrient concentration in grain and straw and enhanced nutriet uptake by rice plants.

In aerobic system of rice cultivation, ammonia is nitrified in the oxidized environment and hence, nitrate is the dominant form of available N (Bouman *et al.,* 2002). An analysis of nitrate reductase (NR) activity in flag leaves was undertaken because this enzyme is involved in nitrogen assimilation by plants. AMF treated rice plants showed higher values of NR activity than the control plants. The AM-upland rice varieties showed about 103% enhanced NR activity than control rice plants. Interestingly, the upland rice genotypes (Pyari and Satyabhama) with highest NR also recorded the highest shoot dry weight and N content compared to uninoculated plants. The interaction between rice genotypes and AM fungi is highly significant (P=0.0001) for NR activity which indicates that mycorrhizal inoculation strongly affected the improvement of NR activity in AM plants.

In the present study, the total chlorophyll content was higher in AMF treated rice plants; this illustrates better photosynthetic efficiency which can be attributed to the better growth observed in AM- colonized plants. A positive correlation between percent colonization and total chlorophyll content ($R^2=0.76$). It has been shown that under water stress conditions, the AM-colonized plants show enhanced photosynthetic efficiency and thus increase in rice shoot biomass (Ruiz-Sanchez *et al.,* 2010). The higher values of chlorophyll content in AMF treated upland rice plants indicate that the photosynthetic apparatus was less affected by the hydric stress generated during intermittent drying periods (Germ *et al.,* 2005). Higher amount of chlorophyll also stimulates production of increased amount of photosynthates in the host plant, which would provide more substrate for the growth and development of root system, AM fungal consortia and rhizospheric microflora (Wu *et al.,* 2010; Li *et al.,* 2017; Hassan *et al.,* 2017). AMF significantly increase the net photosynthesis by increasing the total chlorophyll (Manoharan *et al.,* 2008; Thamizhiniyan *et al.,* 2009). Arbuscularmycorrhizal fungi (AMF) act as a carbon sink as they rely on plant photo assimilates, and may stimulate the photosynthesis rate of the host plant depending on the environmental conditions (Kaschuk *et al.,* 2009). Although there is evidence that the degree of AM root colonization is not necessarily linked to the plant growth responses (Marulanda *et al.,* 2003), in this study we found a positive correlation between the mycorrhizal root lengths achieved and plant growth stimulation. The results obtained in the present study regarding plant nutrient uptake and concentration in grain and straw and protein content in grain evidently indicates that enhanced chlorophyll content and NR activity of rice treated with AMF especially during the peak vegetative growth phase has led to the better plant health and yield response, under aerobic conditions.

This study demonstrated the beneficial effects AM association in rice plants under aerobic conditions. There is considerable potential for using AMF to increase production of aerobic rice. Moreover, AM symbiosis made an important contribution during the early growth phase, when nutrient uptake is limited by the relatively less developed plant root system. We showed that AM association in the early growth stages of rice can have important impact on the nutrient concentration and uptake in later growth stages. Although, mycorrhizal symbiosis could not completely compensate for large yield gap of aerobic rice when compared with flooded rice; but can be considered an important plant strategy for maintaining and improving rice growth under aerobic conditions

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