Strigolactone GR24-mediated mitigation of phosphorus deficiency through mycorrhization in aerobic rice

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ABSTRACT

Strigolactones (SLs) are a new class of plant hormones that play a significant role in regulating various aspects of plant growth promotion, stress tolerance and influence the rhizospheric microbiome. GR24 is a synthetic SL analog used in scientific research to understand the effects of SL on plants and to act as a plant growth promoter. This study aimed to conduct hormonal seed priming at different concentrations of GR24 (0.1, 0.5, 1.0, 5.0 and 10.0 μM with and without arbuscular mycorrhizal fungi (AMF) inoculation in selected aerobic rice varieties (CR Dhan 201, CR Dhan 204, CR Dhan 205, and CR Dhan 207), Kasalath-IC459373 (P-tolerant check), and IR-36 (P-susceptible check) under phosphorus (P)-deficient conditions to understand the enhancement of growth and priming effects in mycorrhization. Our findings showed that seed priming with 5.0 μM SL GR24 enhanced the performance of mycorrhization in CR Dhan 205 (88.91 %), followed by CR Dhan 204 and 207, and AMF sporulation in CR Dhan 201 (31.98 spores / 10 gm soil) and CR Dhan 207 (30.29 spores / 10 g soil), as well as rice growth. The study showed that the highly responsive variety CR Dhan 207 followed by CR Dhan 204, 205, 201, and Kasalath IC459373 showed higher P uptake than the control, and AMF treated with 5.0 μM SL GR24 varieties CR Dhan 205 followed by CR Dhan 207 and 204 showed the best performance in plant growth, chlorophyll content, and soil functional properties, such as acid and alkaline phosphatase activity, soil microbial biomass carbon (MBC), dehydrogenase activity (DHA), and fluorescein diacetate activity (FDA). Overall, AMF intervention with SL GR24 significantly increased plant growth, soil enzyme activity, and uptake of P compared to the control. Under P-deficient conditions, seed priming with 5.0 μM strigolactone GR24 and AMF inoculum significantly increased selected aerobic rice growth, P uptake, and soil enzyme activities. Application of SLs formulations with AMF inoculum in selected aerobic rice varieties, CR Dhan 207, CR Dhan 204, and CR Dhan 205, will play an important role in mycorrhization, growth, and enhancement of P utilization under P- nutrient deficient conditions.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) colonize the majority of plant roots and establish a mutualistic association with them (Besserer et al., 2006), supporting nutrient uptake (Begum et al., 2019), including phosphorus (P) from the soil under P-deficient conditions (Etesami et al., 2021). Under nutrient deficiency conditions in the soil, hormonal priming is used in agriculture to enhance seed germination, seedling emergence, a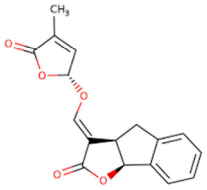nd overall plant performance (Rhaman et al., 2020; Devika et al., 2021; Ibrahim et al., 2022b; Paul et al., 2023). Hormonal priming involves the application of specific plant hormones to seeds before planting to improve their ability to respond to favorable conditions and stress (Rhaman et al., 2020; Mitra et al., 2023b). Plant hormones called strigolactones (SLs) play vital roles in multiple aspects of plant growth and development, including root development, shoot branching, and AMF colonization (Smith, 2014; Mishra et al., 2017; Mitra et al., 2021c). SLs also affect plant responses to environmental cues such as nutrient availability (Marzec et al., 2013).

Table 1
Details of strigolactone GR24 used in this study.

Company name and CAS No	Structure	Chemical formula	Molecular weight	SMILES	Melting point	Storage	Dissolve in
Biosynth Carbosynth Ltd, United Kingdom [76974-79-3]		$C_{17}H_{14}O_5$	298.29 g/mol	CC1=C[C@@H](OC1=O)O/C=C/2\\[C@H]3CC4=CC=CC=C4[C@H]3OC2=O	157 °C	Store at < -15 °C	0.02 % Acetone

SMILES: Simplified molecular-input line-entry system; CAS: Chemical abstract service.

The application of SLs in agriculture and horticulture has gained interest because of their potential to influence plant growth and enhance crop yields (Foo, 2021). Naturally occurring SL signaling or the external application of SLs can potentially improve root system development, leading to better nutrient and water uptake by plants (Marro et al., 2022). SLs suppress shoot branching, directing the plant's energy towards main stem growth, leading to more robust and productive plants with a single dominant stem (Shinohara et al., 2013; Khuvung et al., 2022). SLs promote symbiotic relationships with mycorrhizal fungi, which helps plants increase their nutrient uptake from the soil (Yoneyama, 2019; Soliman et al., 2022; Alvi et al., 2022). The application of SLs can enhance the establishment and effectiveness of beneficial fungal associations (Lanfranco et al., 2018b). SLs are also implicated in plant responses to nutrient stress such as P deficiency (Marzec et al., 2013). SLs are naturally stimulating molecules that hold great potential for investigating plant-soil interactions in both basic and applied science (Bouwmeester et al., 2007; López-Ráez et al., 2011; Kee et al., 2023). Hence, SL can be utilized in agriculture to tackle challenges related to enhancing crop productivity and improving soil health under challenging climatic conditions.

GR-24 is a cost-effective synthetic SL molecule that is commonly used as a reference in SL research and applications (Wigchert et al., 1999; Kgosi et al., 2012; Lachia et al., 2012; Pandya-Kumar et al., 2014; Wang and Xi, 2022). It is commercially available in racemic mixtures as a single enantiomer (Borghi et al., 2021). The structure and stereochemistry of GR-24 mimics those of natural SLs, with an ABC-ring moiety bound to the D-ring *via* an enol ether bridge that activates SL biosynthesis and signaling (Lopez-Obando et al., 2015; Jia et al., 2019; Borghi et al., 2021). The use of SLs improves plant resilience under adverse conditions through SL signal transduction (Foo, 2021). These synthetic compounds can be applied to plants in various ways, including foliar sprays, soil drenches, seed treatments, seed priming, but the timing, concentration, and frequency of application depending on the specific goals and the target plant species. The *rac*-GR24 treatment has no impact on bacterial calcium spiking/ nodulation factor production and growth, but it has been recognized as a plant hormone and play important role in rhizosphere signaling and interaction with AMF (Moscatiello et al., 2010; Soto et al., 2010; Cuyper and Goormachtig, 2017).

Therefore, this study aimed to explore potential methods for improving the association of AMF in four aerobic rice varieties using the check P-susceptible variety and P-tolerant variety by the external application of synthetic SL GR24 at different concentrations through seed priming. This study focused on the development of AMF-SL formulations and the optimum SL concentration to enhance P uptake and rice growth under P-deficient conditions.

2. Materials and methods

2.1. Experimental site

The experiment was conducted during *Rabi* season (2022) in a controlled net house at the Microbiology, Crop Production Division, ICAR- NRRI, Cuttack, India (latitude : 20°25′ N, longitude : 85°55′ E, at an altitude of 24 m above mean sea level). Low phosphorus (6.003 ± 0.59 kg ha^{-1}) soil was collected from Krishi Vigyan Kendra (KVK), Santhpur, ICAR–NRRI, Cuttack, Odisha (20°2745.08N; 85°5258.76E). Each experimental pot was filled with 10 kg homogenized low-P soil.

2.2. Details of strigolactone GR24

Strigolactone GR24 has been purchased from Biosynth Carbosynth®, United Kingdom for the experiment (Table 1).

2.3. Details of AMF inoculum for experiment

The soil-based mixed AMF inoculum was obtained from Microbiology, Crop Production Division, ICAR-NRRI, India. The inoculum contained 130 AMF spores/g of soil, which was multiplied using finger millet (*E. coracana*) and rice as host plants in sterile soil using the trap culture method.

2.4. Seed priming of SL GR24 and experiment description

The pot experiment was conducted with five different concentrations of SL GR24 (T1: 0.1 µM, T2: 0.5 µM, T3: 1.0 µM, T4: 5.0 µM, T5: 10.0 µM, T6: 0.02 % acetone treated, T7: Control) in popular aerobic rice varieties *viz.* V1: CR Dhan 201, V2: CR Dhan 204, V3: CR Dhan 205, V4: CR Dhan 207, V5: P susceptible check (IR 36) and V6: P tolerant check (Kasalath IC459373), with (12,000 spores per pot) and without AMF inoculation under P-deficient conditions. Rice seeds were surface sterilized with a 5 % NaOCl solution, washed 4–5 times with distilled water. The surface sterilized seeds were immersed and primed with GR24 at different concentration, wherein the seed: solution ratio was maintained at 1:5 (w/v). Similar treatment was adopted for acetone treatment and uninoculated control except GR24 priming. Treated seeds were air dried on blotting papers and these primed seeds were then used for experiment. Three plants per pot were maintained with three replication and a CRD design was used. Plant and soil samples were collected after 90 days from each treatment to check the AMF colonization, sporulation, growth parameters, P uptake, soil chemical, microbial, and enzymatic activity analyses.

2.5. Assessment of AMF colonization and spore count

The method developed by Phillip and Hayman (1970) was used to evaluate rice root colonization by AMF (Ganeshamurthy et al., 2017). To commence the procedure, freshly collected root samples were delicately washed to remove soil attached to the root surfaces. The samples were then submerged in a 10 % KOH solution and autoclaved for 15 min at 121 °C. Following autoclaving, the KOH solution was decanted, and the treated roots were rinsed with tap water three times until no brown color appeared in the rinsed water. The root samples were then immersed in a 2 % HCl solution for 5 min, without rinsing with water. The HCl solution

was decanted, and the root samples were stained with 0.05 % trypan blue (HiMedia, India) in lacto-glycerol [lactic acid (400 mL) + glycerol (400 mL)+ water (100 mL)]. The stained samples were then autoclaved for 15 min at 121 °C, after which the staining solution was decanted, and the roots were de-stained with lacto-glycerol solution to remove excess stain. The resulting segments were observed under a compound microscope (Radical RxLr-4, India), and the method proposed by McGonigle et al. (1990) was used to calculate the percentage of root colonization.

AMF root colonization was calculated using the formula:

% of colonization = no. of root segments colonized ÷ total no. of root segments × 100

2.6. Phosphorus estimation in plant sample

The analysis of the P concentration in plant samples was carried out using the vanadomolybdo phosphoric acid method, along with a UV/Vis spectrophotometer (Analytikjena specord-200, Germany) (Arrhenius, 1927). A gram of dried plant material and 10 ml of HNO_3 (69 %) were added and allowed to sit overnight, followed by the addition of 10 ml of tri-acid (HNO_3, H_2SO_4, and $HClO_4$ in a ratio of 9:4:1) and mixing. The mixture was then heated at 100 °C for 1 h, during which time the content reduced to 2–3 ml and turned colorless. The contents were cooled, and 10 ml of HCl (35 %) was added, followed by filtering through Whatman No. 42 filter paper. The filtrate was made up to 100 ml using distilled water, and 5 ml of the filtered sample was taken for the vanadomolybdate reagent (Merck, Germany) and incubated for 30 min. The absorption of the samples was measured at 420 nm using a UV/Vis spectrophotometer, and a standard curve was prepared with a phosphate solution (0.2195 g of KH_2PO_4 in 500 ml distilled water+ 25 ml of 7 N H_2SO_4 and made up to 1000 ml). The P content of the plant samples was calculated from the standard curve.

2.7. Estimation of soil chemical, enzymatic and microbial properties

2.7.1. Acid (AcP) and alkaline (AkP) phosphatases activity

The activity of AcP and AkP phosphatase in soil samples was determined using the method of Tabatabai and Bremner (1969) by incubating a gram of soil in a 50 ml flask with p-nitrophenyl as a substrate, modified universal buffer (MUB) (pH 6.5 for AcP assay and pH 11 for AkP assay), and 0.05 M pNP solution (Nayak et al., 2016). After incubation at 37 °C for 1 h, 1 mL of 0.5 M $CaCl_2$ and 4 mL of 0.5 M NaOH were added, and the resulting yellow color was measured using a spectrophotometer. A standard curve was prepared with p-nitrophenol, and the amount of p-nitrophenol liberated was calculated to determine the phosphatase activity, expressed in l g of p-nitrophenyl phosphate (pNP) released per gram of soil per hour. Phosphatase activity was calculated as µg p-nitrophenol (pNP) g^{-1} h^{-1}.

2.7.2. Soil microbial biomass carbon (MBC)

The chloroform fumigation extraction (CFE) method was used to determine the activity of microbial biomass carbon (MBC) using the method of Witt et al. (2000). 10 g of moist soil samples were collected and kept in oven at 105 °C for 24 h, and moisture content was calculated. A 50 ml beaker was taken and 3 g of soil was placed in a beaker (2 sets). One set was un-fumigated, while the other was fumigated in a vacuum desiccator. A vacuum was created inside the desiccator until the chloroform boiled. The desiccators were maintained in the dark for 24 h. Both fumigated and un-fumigated samples were transferred to a 250 ml conical flask and 25 ml of 0.5 M K_2SO_4 was added. The total organic carbon (TOC) content in the soil extracts was measured using the dichromate digestion method (Schumacher, 2002). The CFE-MBC was calculated as 2.64 times the difference in extractable organic C between fumigated and unfumigated soils and expressed as µg g^{-1} soil (Vance

et al., 1987).

2.7.3. Soil dehydrogenase activity (DHA)

The dehydrogenase activity (DHA) was measured using the method described by Casida et al. (1964), which involved the use of triphenyltetrazolium chloride (TTC) as a substrate. The soil samples (3 g) were mixed with 0.2 g of $CaCO_3$, 1 ml of 3 % (w/v) 2,3,5-TTC, 2.5 ml of distilled water, and incubated at 37 ºC for 24 h. After incubation, 10 ml of methanol were added, and the enzyme converted TTC to 2,3,5 triphenylformazan (TPF). The TPF formed was extracted with methanol, the extracts were filtered, and absorption was measured at 485 nm using a spectrophotometer (Analytikjena specord-200, Germany) and expressed as µg TPF h^{-1} g^{-1} soil (Nayak et al., 2016).

2.7.4. Soil fluorescein diacetate activity (FDA)

Soil fluorescein diacetate activity (FDA) measurements were performed using the method of Schnrer and Rosswall (1982), as modified by Adam and Duncan (2001). The amount of fluorescein released during the assay was determined using a calibration graph created with a 0–5 µg fluorescein mL^{-1} standard, and it was reported in units of µg fluorescein h^{-1} g^{-1} soil (Nayak et al., 2016).

2.8. Measures relative chlorophyll content of leaves

A chlorophyll meter (SPAD 502 Plus; Konica Minolta, Japan) was used to measure the relative chlorophyll content of the leaves (greenness) without damaging the leaves in each treatment. Reading was taken between 10:30–13.00 h of the day.

2.9. Statistical analysis

The study adopted a Completely Randomized Design (CRD) incorporating three independent factors labelled as Factor A, Factor B, and Factor C. Each factor comprised multiple levels, resulting in a total of $r \times s \times t$ treatment combinations. The experiment was replicated three times to minimize experimental error. A three-way analysis of variance (ANOVA) was conducted to ascertain the influence of Factors A, B, and C on the response variable(s). The ANOVA model was fitted to the data utilizing the aov() function available in the R statistical computing environment (Team, R.C.., 2000). The data obtained were statistically analyzed using the Web-Based Agricultural Statistical Software Package (WASP 2.0) developed by the Central Coastal Agricultural Research Institute (ICAR), Ela Goa (www.ccari.res.in/waspn ew.html).

3. Results and discussion

3.1. Effect of strigolactone GR24 application with and without AMF inoculation on shoot and root length in different rice varieties under P deficiency

Strigolactones (SLs) are a group of plant hormones that control various aspects of plant development, including shoot and root growth (Agusti et al., 2011). The use of synthetic strigolactones such as GR24, *rac*-GR24, GR7, AB01, *mimic* T-010, 5-Deoxystrigol, 2′-Epi-5-deoxystrigol, RMS1, and *Nijmegen*-1 can affect plant growth and architecture (Xie et al., 2013; Zwanenburg et al., 2013; Yamada et al., 2014; Vurro et al., 2016; Sun et al., 2021; Ahsan et al., 2022). The effects of synthetic SLs on shoot duration vary depending on SL application concentration (Ruyter-Spira et al., 2011). It is crucial to remember that these effects depend on the concentrations and may differ depending on plant variety. According to many research, low concentrations of GR24 (10 nM, 0.1–5.0 µM) can promote shoot branching and elongation, increasing the length of the shoot (Kapulnik et al., 2011; De Cuyper et al., 2015; Jiu et al., 2022; Wani et al., 2023). This response is related to the hormone's support for the shoot architecture and growth. Higher concentrations of GR24, synthetic SL analogs, or prolonged exposure may lead to shoot

Table 2

Effect of strigolactone GR24 on rice growth with and without application of AMF under low P available soil.

Treatments	Rice varieties	Shoot length (cm)		Root length (cm)	
		With AMF	Without AMF	With AMF	Without AMF
0.1 μM GR24	CR Dhan 201	61.644[e]	60.203[e]	13.935[d]	13.461[c]
	CR Dhan 204	62.039[d]	60.597[d]	15.759[b]	14.953[b]
	CR Dhan 205	62.839[c]	61.394[cd]	14.731[c]	12.538[d]
	CR Dhan 207	66.157[b]	64.702[b]	13.337[e]	12.927[d]
	IR36	59.023[f]	57.590[f]	11.277[f]	10.484[e]
	Kasalath IC459373	75.015[a]	73.534[a]	17.359[a]	16.547[a]
CD(0.05)		**0.283**	**0.333**	**0.104**	**0.122**
0.5 μM GR24	CR Dhan 201	66.448[c]	65.694[b]	13.387[d]	12.588[c]
	CR Dhan 204	60.935[e]	59.494[de]	14.432[c]	13.630[b]
	CR Dhan 205	61.578[d]	60.137[d]	16.523[a]	15.714[a]
	CR Dhan 207	67.152[b]	64.993[c]	16.423[b]	15.614[a]
	IR36	59.163[f]	57.729[f]	12.282[e]	11.486[d]
	Kasalath IC459373	78.197[a]	76.706[a]	12.342[e]	11.546[d]
CD(0.05)		**0.347**	**0.409**	**0.095**	**0.112**
1.0 μM GR24	CR Dhan 201	58.028[e]	56.598[e]	14.373[d]	13.570[d]
	CR Dhan 204	61.094[d]	59.654[d]	14.432[d]	13.630[d]
	CR Dhan 205	69.275[b]	67.811[bd]	15.925[c]	15.118[bc]
	CR Dhan 207	68.578[bc]	67.116[c]	16.264[b]	15.456[b]
	IR36	68.121[c]	66.660[c]	12.382[e]	11.585[e]
	Kasalath IC459373	87.191[a]	85.673[a]	16.423[a]	15.614[a]
CD(0.05)		**0.506**	**0.597**	**0.077**	**0.091**
5.0 μM GR24	CR Dhan 201	60.934[e]	59.495[b]	14.482[b]	13.678[b]
	CR Dhan 204	62.308[d]	60.865[f]	14.383[c]	13.580[cd]
	CR Dhan 205	62.739[c]	61.295[e]	16.373[a]	15.565[a]
	CR Dhan 207	71.531[b]	70.060[c]	14.482[b]	13.679[b]
	IR36	59.163[f]	57.729[d]	13.158[e]	12.360[de]
	Kasalath IC459373	81.505[a]	80.004[a]	13.238[d]	12.439[d]
CD(0.05)		**0.427**	**0.504**	**0.058**	**0.069**
10.0 μM GR24	CR Dhan 201	76.083[b]	74.599[f]	14.930[e]	14.126[e]
	CR Dhan 204	62.573[f]	61.129[e]	18.248[c]	17.434[c]
	CR Dhan 205	67.185[e]	65.727[d]	21.131[a]	20.308[a]
	CR Dhan 207	72.988[c]	71.513[b]	16.254[d]	15.446[de]
	IR36	68.121[d]	66.660[c]	12.342[f]	11.546[f]
	Kasalath IC459373	83.143[a]	81.638[a]	20.345[b]	19.524[bc]
CD(0.05)		**0.365**	**0.431**	**0.167**	**0.197**
Acetone treated	CR Dhan 201	62.039[f]	60.597[f]	12.381[c]	11.584[c]
	CR Dhan 204	63.270[e]	61.824[e]	13.377[ab]	12.578[bc]
	CR Dhan 205	64.299[d]	62.849[de]	12.379[b]	11.585[c]
	CR Dhan 207	66.223[b]	64.768[b]	12.382[c]	11.583[c]
	IR36	65.035[c]	63.584[c]	11.287[d]	9.494[d]
	Kasalath IC459373	79.075[a]	77.582[a]	14.263[a]	13.461[a]
CD(0.05)		**0.312**	**0.368**	**0.051**	**0.06**
Control	CR Dhan 201	60.944[d]	59.505[d]	11.178[a]	10.385[a]
	CR Dhan 204	63.077[b]	61.632[b]	10.282[c]	9.492[c]
	CR Dhan 205	62.407[c]	60.964[cd]	10.949[b]	10.157[b]
	CR Dhan 207	60.934[d]	59.495[d]	9.286[d]	8.499[cd]
	IR36	61.084[d]	59.644[d]	10.252[c]	9.462[c]
	Kasalath IC459373	71.883[a]	70.411[a]	11.168[ab]	10.375[a]
CD(0.05)		**0.212**	**0.250**	**0.037**	**0.043**

Different lowercase letters represent significant variations among the treatment at $p < 0.05$, CD: critical difference.

elongation (Krasylenko et al., 2021). This is frequently linked to changes in the physiological responses of plants, which may entail feedback-regulatory processes. Plant growth depends on auxin transport status, which is supported by the combined effects of synthetic SL and AM symbiosis (Mitra et al., 2021a,b; Alvi et al., 2022; Kountche et al., 2018). The ability of GR24 to promote shoot and root elongation may be complemented by the capacity of AMF to enhance nutrient uptake. However, it is also possible that these two factors can be combined intricately. This precise result might be influenced by the complex interplay between GR24- and AMF-induced plant hormone signaling, nutrient availability, and growth responses. According to the present research findings, Kasalath IC459373 shown higher performance in shoot growth at the concentrations of 1.0 μM (87.191 cm) and 10.0 μM (83.143 cm) GR24 SL with combination application of AMF (Table 2). However, the priming of SL GR24 at concentrations of 5.0 and 10.0 μM for CR Dhan 207 (71.531 cm), CR Dhan 201 (76.083 cm), respectively and 1.0 μM for CR Dhan 205 (69.275 cm) resulted significant increase in shoot growth under P deficient conditions (Table 2). Where as in, CR

Dhan 205 (21.131 cm) and Kasalath IC459373 (20.345 cm) the highest performance in root growth was observed at the concentration of 10.0 μM GR24 SL with AMF inoculated treatment (Supplementary Table 1). However, application of GR24 concentration with 5.0 and 10.0 μM in CR Dhan 207 and CR Dhan 205 showed significantly higher root growth as compared to the un-inoculated AMF control (Table 2). Similar results have also been found with the exogenous application of various concentrations of GR24 (0.01, 0.1, 1.0, and 10 μM) was performed with 1/2 Murashige and Skoog medium (0.8 % agar and 3 % sucrose) for plant growth (Arite et al., 2012). Similarly, increased primary root length and enhanced root system architecture have been observed in *Arabidopsis* treated with 1.25 μM GR24 (Ruyter-Spira et al., 2011). These findings suggest that SLs positively influence root length, and that the effect of GR24 on rice growth varies from variety to variety.

Table 3

Strigolactone GR24 seed priming and its effect on P uptake in different rice varieties with and without application AMF under P deficient condition.

Treatments	Rice varieties	Plant P (g. pot^{-1})	
		With AMF	Without AMF
0.1 μM GR24	CR Dhan 201	16.863[b]	16.370[b]
	CR Dhan 204	16.186[c]	15.700[cd]
	CR Dhan 205	15.235[e]	14.758[e]
	CR Dhan 207	18.788[a]	18.276[a]
	IR36	13.150[f]	12.693[e]
	Kasalath IC459373	15.813[d]	15.331[f]
CD(0.05)		**0.093**	**0.084**
0.5 μM GR24	CR Dhan 201	15.251[f]	14.774[f]
	CR Dhan 204	18.661[c]	18.151[c]
	CR Dhan 205	20.622[b]	20.093[a]
	CR Dhan 207	17.005[d]	16.511[b]
	IR36	16.875[e]	16.382[ab]
	Kasalath IC459373	21.065[a]	20.532[a]
CD(0.05)		**0.114**	**0.104**
1.0 μM GR24	CR Dhan 201	14.994[e]	14.519[f]
	CR Dhan 204	17.901[b]	17.398[b]
	CR Dhan 205	16.099[d]	15.614[d]
	CR Dhan 207	16.937[c]	16.443[c]
	IR36	14.478[f]	14.009[ef]
	Kasalath IC459373	21.741[a]	21.201[a]
CD(0.05)		**0.131**	**0.119**
5.0 μM GR24	CR Dhan 201	20.127[d]	19.603[ab]
	CR Dhan 204	19.601[e]	19.082[ab]
	CR Dhan 205	22.634[b]	22.085[b]
	CR Dhan 207	20.411[c]	19.884[ab]
	IR36	16.484[f]	15.995[c]
	Kasalath IC459373	25.731[a]	25.152[a]
CD(0.05)		**0.155**	**0.141**
10.0 μM GR24	CR Dhan 201	24.631[a]	24.063[a]
	CR Dhan 204	18.054[e]	17.550[cd]
	CR Dhan 205	19.977[c]	19.454[c]
	CR Dhan 207	18.217[d]	17.711[cd]
	IR36	16.186[f]	15.700[d]
	Kasalath IC459373	21.360[b]	20.823[b]
CD(0.05)		**0.149**	**0.135**
Acetone treated	CR Dhan 201	15.252[f]	14.775[d]
	CR Dhan 204	19.009[b]	18.495[b]
	CR Dhan 205	18.760[c]	18.249[b]
	CR Dhan 207	18.418[d]	17.910[cd]
	IR36	16.186[e]	15.700[d]
	Kasalath IC459373	21.902[a]	21.361[a]
CD(0.05)		**0.117**	**0.106**
Control	CR Dhan 201	12.746[f]	12.005[d]
	CR Dhan 204	14.327[b]	13.860[c]
	CR Dhan 205	13.937[c]	13.473[c]
	CR Dhan 207	13.764[d]	13.302[c]
	IR36	12.934[e]	15.586[b]
	Kasalath IC459373	16.790[a]	15.976[a]
CD(0.05)		**0.073**	**0.058**

Different lowercase letters represent significant variations among the treatment at $p < 0.05$.

3.2. Influence of SL-GR24 application with and without AMF inoculation on P-uptake in different rice varieties

AMF, especially for P uptake, are beneficial soil microorganisms that colonize plant roots to improve nutrient uptake (Perner et al., 2007; Silva et al., 2023). According to Andreo-Jimenez et al. (2015), SL plays a crucial role as a modulator of the coordinated growth of plants in response to nutrient-deficient conditions, particularly phosphorus scarcity. In addition to controlling root architecture belowground, they serve as chemical cues that allow plants to communicate with their surroundings. In the present study, we investigated the effects of different concentrations of SL-GR24 and seed priming in different rice varieties on P uptake with and without AMF inoculation. According to Czarnecki et al. (2013), SLs play dual roles in plant P uptake and utilization. This has resulted in the emergence of a signaling module that shows how P uptake, plant-microbe symbiotic relationships, and plant design are all controlled together. Seed priming with 5.0 μM GR24 and AMF inoculum resulted in the highest P uptake in Kasalath IC459373

(25.731 g pot^{-1}), followed by CR Dhan 201 (24.631 g pot^{-1}), and CR Dhan 205 (22.634 g pot^{-1}) compared to the un-inoculated control. Application of 5.0 μM GR24 may attract and enhance colonization of AMF in roots and could improve nutrient uptake, particularly phosphorus. Thus, signaling for mycorrhizal interactions can be improved by SL-GR24 application, which increases AMF colonization (Makhzoum et al., 2017; Kowalczyk and Hrynkiewicz, 2018; Kaniganti et al., 2022). This combination could have a synergistic effect on nutrient uptake, in addition to the ability of AMF to enhance P uptake in aerobic rice under P-deficient conditions. Overall, in all varieties, the optimum concentration of 5.0 μM SL GR24 strongly influenced the P uptake under P-deficient conditions (Table 3; Supplementary Table 1).

3.3. Impact of SL-GR24 application with and without AMF inoculation on its sporulation and colonization in different rice varieties

Numerous SL activities and applications have been documented in AMF symbiosis under different crop cultivation conditions (Lanfranco

Table 4

Strigolactone GR24 priming effect on AMF sporulation and colonization in different rice varieties with and without application AMF under P deficient soil.

Treatments	Rice varieties	AMF sporulation (spores / 10 gm soil)		% of AMF colonization	
		With AMF	Without AMF	With AMF	Without AMF
0.1 µM GR24	CR Dhan 201	19.273[e]	7.053	67.118[b]	6.731
	CR Dhan 204	21.997[c]	4.826	62.939[c]	2.886
	CR Dhan 205	21.132[d]	3.944	67.016[b]	7.521
	CR Dhan 207	23.221[b]	7.086	53.191[e]	NC
	IR36	19.240[e]	2.019	59.056[b]	NC
	Kasalath IC459373	24.216[a]	6.072	77.967[a]	NC
CD(0.05)		**0.102**	**NS**	**0.42**	**NS**
0.5 µM GR24	CR Dhan 201	26.207[b]	9.112	67.009[c]	7.037
	CR Dhan 204	23.333[e]	6.184	68.014[b]	8.406
	CR Dhan 205	24.316[d]	10.136	58.051[e]	NC
	CR Dhan 207	25.321[c]	8.210	69.009[a]	7.737
	IR36	21.230[f]	4.046	58.058[e]	NC
	Kasalath IC459373	27.212[a]	7.187	59.053[d]	NC
CD(0.05)		**0.107**	**NS**	**0.266**	**NS**
1.0 µM GR24	CR Dhan 201	25.336[b]	4.060	67.109[b]	7.111
	CR Dhan 204	24.226[c]	7.096	59.053[e]	NC
	CR Dhan 205	23.331[d]	6.184	62.935[b]	3.037
	CR Dhan 207	21.244[e]	8.226	66.023[c]	6.364
	IR36	20.346[f]	3.144	59.053[e]	NC
	Kasalath IC459373	27.312[a]	10.237	68.014[a]	7.447
CD(0.05)		**0.129**	**NS**	**0.198**	**NS**
5.0 µM GR24	CR Dhan 201	31.983[a]	14.993	70.997[e]	11.330
	CR Dhan 204	29.303[c]	12.264	83.837[b]	NC
	CR Dhan 205	28.267[d]	11.21	88.913[a]	8.813
	CR Dhan 207	30.298[b]	13.277	78.960[c]	NC
	IR36	21.244[f]	4.060	69.006[f]	7.781
	Kasalath IC459373	26.317[e]	9.224	74.981[d]	12.039
CD(0.05)		**0.188**	**NS**	**0.382**	**NS**
10.0 µM GR24	CR Dhan 201	23.336[d]	6.184	59.053[f]	NC
	CR Dhan 204	21.240[e]	4.056	68.977[d]	8.727
	CR Dhan 205	25.222[c]	8.109	70.997[c]	10.371
	CR Dhan 207	28.307[b]	11.25	77.964[a]	3.021
	IR36	29.297[a]	12.258	68.011[e]	NC
	Kasalath IC459373	29.306[a]	12.267	75.977[b]	17.761
CD(0.05)		**0.169**	**NS**	**0.335**	**NS**
Acetone treated	CR Dhan 201	23.334[c]	6.187	69.007[c]	NC
	CR Dhan 204	28.311[b]	11.254	71.010[b]	10.450
	CR Dhan 205	23.332[c]	6.184	75.977[a]	NC
	CR Dhan 207	22.335[d]	5.17	69.009[c]	NC
	IR36	21.201[e]	4.015	65.025[d]	14.408
	Kasalath IC459373	29.307[a]	12.268	70.997[b]	11.041
CD(0.05)		**0.167**	**NS**	**0.179**	**NS**
Control	CR Dhan 201	21.174[b]	4.988	60.952[c]	2.376
	CR Dhan 204	20.241[c]	3.038	62.082[b]	5.783
	CR Dhan 205	20.235[c]	10.159	59.053[d]	NC
	CR Dhan 207	27.235[a]	3.032	60.940[c]	2.369
	IR36	21.121[b]	3.934	58.058[e]	NC
	Kasalath IC459373	27.246[a]	2.465	69.020[a]	3.491
CD(0.05)		**0.17**	**NS**	**0.193**	**NS**

Different lowercase letters represent significant variations among the treatment at $p < 0.05$; NC: no AMF colonization.
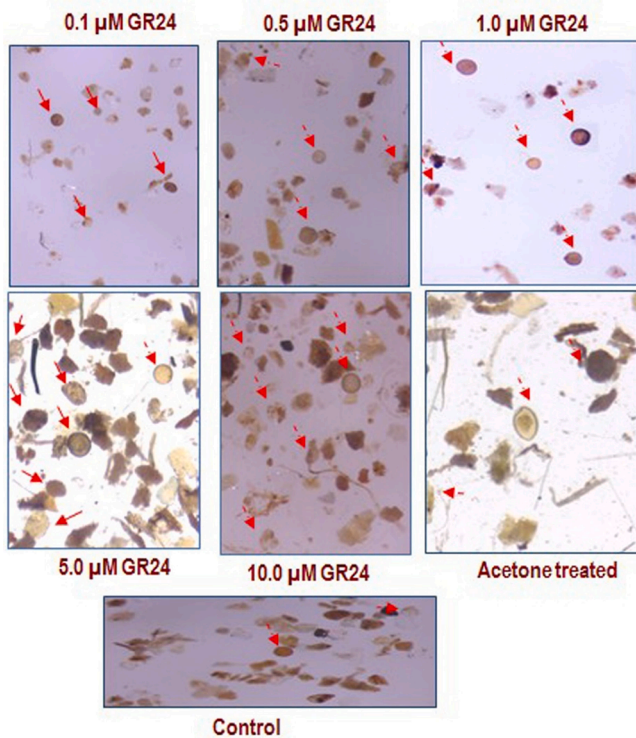
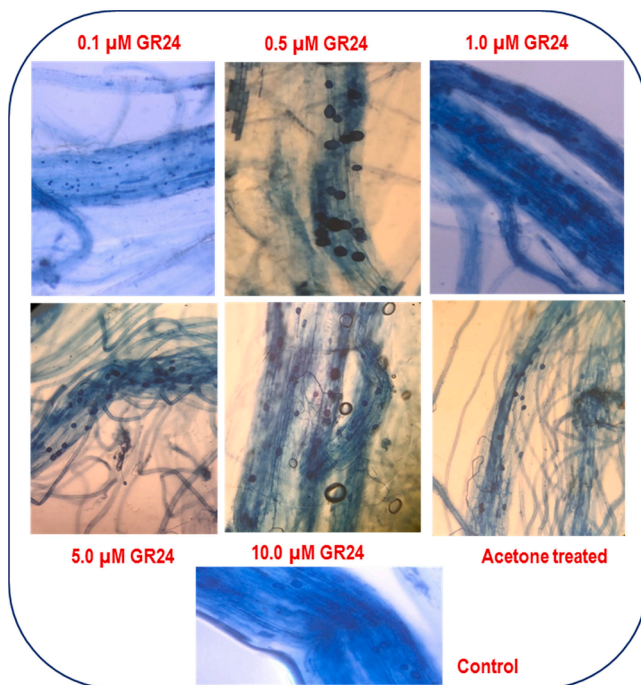**Fig. 1.** Sporulation of AMF in rice varieties treated with SL GR24.

Fig. 2. AMF colonization in different rice varieties treated with SL GR24.

et al., 2018b; Kim et al., 2022; Soliman et al., 2022). When P is limited to the soil, AMF intervention has an important impact on P utilization, soil enzyme activities, and rice growth. To address this nutrient limitation, SLs also contribute to the modification of root architecture *via* AMF symbiosis. The activation of the symbiotic relationship with mycorrhizal fungi is an adaptation to improve the uptake of mineral nutrients, in which SLs play a vital role not as plant hormones but as rhizosphere signaling molecules (Besserer et al., 2006). SLs help AMF to branch their

hyphal structures, which promotes the growth of a mutually beneficial relationship (Akiyama et al., 2005). In the present study, application of AMF with 5.0 μM SL GR24 resulted in maximum AMF sporulation in CR Dhan 201 (31.98 spores / 10 gm soil) and CR Dhan 207 (30.29 spores / 10 g soil) (Table 4; Fig. 1; Supplementary Table 1). Similarly, the percentage of AMF colonization was significantly higher in CR Dhan 205 (88.91 %), followed by CR Dhan 204 (83.83 %), and CR Dhan 207 (78.96 %) (Table 4; Fig. 2; Supplementary Table 1).

3.4. Effect of GR24 priming with and without AMF inoculation on soil functional properties viz. MBC, FDA and DHA in different rice varieties

The quantifiable terrestrial labile carbon (C) component, known as microbial biomass carbon (MBC), was used to measure the soil biological activity (Wei et al., 2022). The main determining factors of MBC are soil organic carbon (SOC), water retention capability, and soil pH. MBC contributes approximately 1 –5 % C to the total SOC (Babur and Dindaroglu, 2020). Host plants provide nutrition to AMF in exchange for the carbohydrates produced during photosynthesis (Panneerselva et al., 2019; Salmeron-Santiago et al., 2021). The hyphal network of AMF can also transport soil nutrients to plants and enhance soil quality by strengthening the soil structure and its ability to retain water (Begum et al., 2019; Schütz et al., 2022). AMF are essential for P/C cycling and SOC utilization, enhancing resistance and assisting in the growth of plants under P-deficient conditions for ecosystem restoration (Begum et al., 2019; Etesami et al., 2021; Shen et al., 2023). In the present study, MBC varied with the different levels of SL GR24 and AMF. Compared to the uninoculated control, 0.5, 5.0, and 10.0 μM concentrations of GR24 treated seeds in CR Dhan 205 (485.086, 495.065, and 496.150 μg g^{-1} soil, respectively) resulted in higher soil MBC (Table 5; Supplementary Table 1). The soil fluorescein diacetate activity (FDA) hydrolysis assay, which analyzes the enzyme activity of soil microbes, can quantify the total amount of microbial activity in an environmental sample reported by numerous researchers (Schnrer and Rosswall, 1982; Patle et al., 2018; Panneerselvam et al., 2019). FDA and dehydrogenase enzyme activities have been reported to improve by 46.50 % and 43.70 %, respectively, with the application of AMF treatment (Jabborova et al., 2021). This study aimed to understand the effects of SL GR24 priming on the FDA in different rice varieties under P-deficient conditions. SL GR24 priming with AMF inoculation showed higher FDA at 5.0 μM GR24 treated Kasalath IC459373 (8.785 μg fluorescein h^{-1} g^{-1} soil) and 0.5 μM GR24 treated CR Dhan 204 (8.347 μg fluorescein h^{-1} g^{-1} soil) (Table 5; Supplementary Table 1). However, FDA activity in all aerobic rice varieties was lower in the 0.1 μM GR24 treatment, whereas 5.0 μM GR24 showed a higher response to AMF inoculation. Soil dehydrogenase activity (DHA) is frequently used as an indicator of cellular metabolic activity, because it catalyzes the removal of hydrogen atoms from organic molecules. This allowed for the assessment of specific dehydrogenase activities, providing insights into both soil health and microbial cell function (Wolińska and Stępniewska, 2012). Soil microbes and AMF can affect soil dehydrogenase activity by enhancing nutrient cycling and promoting microbial growth (Panneerselvam et al., 2019). According to Raghavendra et al. (2020), sodium alginate with an AMF-based product exhibited the highest dehydrogenase activity (5.12 g TPF produced g^{-1} soil d^{-1}) after 45 days of growth. The main aim of this study was to understand the effects of AMF intervention with hormonal priming on soil DHA in different rice varieties. The results showed that 5.0 and 10.0 μGR24 treated CR Dhan 207 resulted in higher DHA with and without AMF treatments (Supplementary Table 1). DHA showed an effective response to AMF inoculation in all aerobic rice varieties, as well as Kasalath IC459373 at a lower dose of 0.1 μM GR24 (Table 5).

3.5. Effect of GR24 priming with and without AMF inoculation on AcP and AkP activity in different rice varieties

Soil phosphatase is an enzyme that catalyzes soil organic phosphate

Table 5

Strigolactone GR24 effect on soil functional properties *viz*. MBC, FDA and DHA in different rice varieties with and without application AMF inoculum under P deficient soil.

Treatments	Rice varieties	MBC ($\mu g\ g^{-1}$ soil)		FDA (μg fluorescein $h^{-1}\ g^{-1}$ soil)		DHA (μgTPF $h^{-1}\ g^{-1}$ soil)	
		With AMF	**Without AMF**	**With AMF**	**Without AMF**	**With AMF**	**Without AMF**
0.1 µM GR24	CR Dhan 201	402.596[d]	385.887[d]	6.335[b]	5.097[d]	21.055[b]	19.638[b]
	CR Dhan 204	421.499[a]	402.701[b]	6.335[b]	5.039[c]	21.082[b]	20.781[a]
	CR Dhan 205	421.488[a]	404.779[ab]	7.342[a]	6.382[a]	20.236[c]	18.755[c]
	CR Dhan 207	419.410[b]	404.789[a]	6.346[b]	5.386[ab]	21.121[b]	19.708[b]
	IR36	399.503[e]	382.794[e]	5.999[c]	5.375[ab]	22.226[a]	20.757[ab]
	Kasalath IC459373	406.468[c]	389.759[c]	6.356[b]	5.325[b]	21.012[b]	19.993[b]
CD(0.05)		**0.504**	**0.514**	**0.023**	**0.026**	**0.285**	**0.243**
0.5 µM GR24	CR Dhan 201	432.338[c]	415.629[c]	7.349[b]	6.389[b]	20.235[c]	18.739[c]
	CR Dhan 204	461.114[b]	444.405[ab]	8.347[a]	7.287[a]	21.045[b]	19.693[b]
	CR Dhan 205	485.086[a]	468.377[a]	7.302[c]	7.142[a]	21.072[b]	20.671[a]
	CR Dhan 207	407.851[e]	391.142[b]	6.344[e]	5.384[c]	18.398[d]	16.855[d]
	IR36	407.453[e]	390.744[b]	6.828[d]	5.868[c]	21.345[a]	19.829[b]
	Kasalath IC459373	414.407[d]	397.698[d]	7.349[b]	6.219[b]	21.284[ab]	19.815[b]
CD(0.05)		**1.596**	**1.369**	**0.033**	**0.031**	**0.272**	**0.258**
1.0 µM GR24	CR Dhan 201	434.340[b]	417.631[bc]	6.306[d]	5.413[b]	22.369[b]	21.950[a]
	CR Dhan 204	474.153[a]	457.444[a]	7.505[a]	6.478[a]	23.365[a]	20.928[b]
	CR Dhan 205	420.780[d]	404.071[d]	6.347[d]	5.387[b]	20.281[e]	18.786[d]
	CR Dhan 207	421.775[d]	405.067[d]	6.356[c]	5.462[b]	21.183[d]	19.712[c]
	IR36	427.466[c]	410.757[c]	7.202[c]	6.242[a]	20.288[e]	18.793[d]
	Kasalath IC459373	411.415[e]	394.706[e]	6.344[b]	5.417[b]	21.274[c]	19.805[c]
CD(0.05)		**1.106**	**1.106**	**0.027**	**0.209**	**0.060**	**0.048**
5.0 µM GR24	CR Dhan 201	422.482[d]	405.773[d]	6.354[e]	5.413[c]	20.280[f]	18.785[e]
	CR Dhan 204	427.372[c]	410.663[c]	6.950[d]	6.000[b]	21.236[e]	19.766[d]
	CR Dhan 205	495.065[a]	478.356[a]	7.349[b]	7.139[a]	22.370[c]	20.929[c]
	CR Dhan 207	436.330[b]	419.621[ab]	6.191[f]	5.231[c]	24.261[a]	21.921[b]
	IR36	421.675[d]	404.966[d]	7.302[c]	6.311[b]	21.735[d]	20.278[c]
	Kasalath IC459373	426.361[c]	409.652[c]	8.785[a]	7.387[a]	23.337[b]	22.869[a]
CD(0.05)		**1.414**	**1.123**	**0.046**	**0.049**	**0.072**	**0.057**
10.0 µM GR24	CR Dhan 201	421.500[e]	409.791[d]	7.339[a]	6.383[a]	25.228[f]	23.860[a]
	CR Dhan 204	422.495[e]	405.786[e]	6.306[c]	5.316[c]	23.365[e]	21.950[c]
	CR Dhan 205	496.150[a]	479.441[a]	6.344[c]	5.384[c]	24.350[c]	22.961[a]
	CR Dhan 207	484.076[b]	467.367[ab]	7.329[a]	6.352[ab]	24.260[a]	22.868[b]
	IR36	480.509[c]	463.800[c]	7.339[a]	6.169[b]	21.174[d]	19.702[d]
	Kasalath IC459373	426.377[d]	409.668[d]	6.354[b]	5.394[c]	21.183[b]	19.711[d]
CD(0.05)		**1.755**	**1.252**	**0.027**	**0.053**	**0.086**	**0.068**
Acetone treated	CR Dhan 201	427.373[c]	410.664[c]	7.339[b]	6.381[b]	20.279[a]	18.784[d]
	CR Dhan 204	425.491[d]	408.782[d]	6.344[d]	5.383[c]	20.243[d]	18.747[d]
	CR Dhan 205	424.385[d]	407.677[cd]	8.334[a]	7.374[a]	20.241[b]	18.745[d]
	CR Dhan 207	425.470[d]	408.761[d]	6.831[c]	5.879[c]	21.274[c]	19.805[c]
	IR36	480.125[b]	463.416[b]	7.339[b]	6.365[ab]	23.265[e]	21.847[b]
	Kasalath IC459373	495.065[a]	478.356[a]	6.344[d]	5.392[c]	24.261[e]	22.869[a]
CD(0.05)		**1.613**	**1.619**	**0.038**	**0.041**	**0.088**	**0.069**
Control	CR Dhan 201	390.499[e]	373.790[e]	5.935[e]	4.953[c]	17.943[f]	16.388[d]
	CR Dhan 204	399.162[d]	382.453[d]	5.999[c]	5.022[ab]	19.293[d]	17.773[c]
	CR Dhan 205	418.339[a]	401.630[a]	6.005[b]	5.012[c]	19.193[e]	17.670[c]
	CR Dhan 207	409.453[c]	392.744[c]	6.109[a]	5.149[a]	20.289[b]	18.794[b]
	IR36	399.437[d]	382.728[d]	5.986[d]	5.081[b]	19.930[c]	18.426[b]
	Kasalath IC459373	417.417[b]	400.708[ab]	5.998[c]	5.029[ab]	20.884[a]	19.405[a]
CD(0.05)		**0.557**	**0.556**	**0.003**	**0.083**	**0.051**	**0.040**

Different lowercase letters represent significant variations among the treatment at $p < 0.05$.

Table 6

Strigolactone GR24 application effect on soil AcP activity in different rice varieties with and without application of AMF under P deficient soil.

Treatments	Rice varieties	AcP (µg *p*-nitrophenol released.g^{-1} soil h^{-1})		AkP (µg *p*-nitrophenol released g^{-1} soil h^{-1})	
		With AMF	Without AMF	With AMF	Without AMF
0.1 µM GR24	CR Dhan 201	28.300[b]	18.281[d]	19.263[d]	18.614[b]
	CR Dhan 204	27.249[d]	20.195[a]	21.177[a]	20.195[a]
	CR Dhan 205	28.254[c]	18.301[d]	19.283[d]	18.635[b]
	CR Dhan 207	29.228[a]	19.283[b]	20.265[b]	19.283[b]
	IR36	27.248[d]	18.908[c]	19.890[c]	19.241[b]
	Kasalath IC459373	28.244[c]	20.192[a]	21.174[a]	20.192[a]
CD(0.05)		**0.037**	**0.043**	**0.043**	**0.758**
0.5 µM GR24	CR Dhan 201	29.249[d]	22.244[b]	23.226[b]	22.244[a]
	CR Dhan 204	31.107[c]	23.278[a]	24.260[a]	22.945[a]
	CR Dhan 205	29.249[d]	18.291[d]	19.273[d]	18.624[b]
	CR Dhan 207	28.255[e]	19.293[c]	20.275[c]	19.293[b]
	IR36	31.190[b]	19.307[c]	20.289[c]	19.173[b]
	Kasalath IC459373	32.232[a]	19.309[c]	20.624[c]	19.309[b]
CD(0.05)		**0.076**	**0.099**	**0.422**	**0.901**
1.0 µM GR24	CR Dhan 201	33.131[a]	20.192[d]	21.174[d]	20.192[c]
	CR Dhan 204	29.239[c]	21.267[c]	22.249[c]	20.600[c]
	CR Dhan 205	27.249[d]	18.303[e]	19.285[e]	18.636[d]
	CR Dhan 207	29.226[c]	22.285[b]	23.267[b]	21.952[b]
	IR36	31.130[b]	20.271[d]	21.253[d]	20.605[c]
	Kasalath IC459373	29.228[c]	23.281[a]	24.262[a]	23.281[a]
CD(0.05)		**0.101**	**0.087**	**0.087**	**1.147**
5.0 µM GR24	CR Dhan 201	28.243[e]	23.456[b]	24.438[b]	23.457[b]
	CR Dhan 204	31.207[b]	20.192[d]	21.174[d]	21.092[cd]
	CR Dhan 205	33.120[a]	19.293[e]	20.275[e]	19.293[e]
	CR Dhan 207	31.229[b]	22.285[c]	23.267[c]	21.952[c]
	IR36	29.239[d]	20.255[d]	21.237[d]	20.255[d]
	Kasalath IC459373	30.244[c]	24.273[a]	25.255[a]	24.273[a]
CD(0.05)		**0.085**	**0.100**	**0.100**	**0.816**
10.0 µM GR24	CR Dhan 201	31.229[c]	19.296[d]	20.278[d]	19.629[c]
	CR Dhan 204	33.197[a]	20.292[c]	21.274[c]	20.292[bc]
	CR Dhan 205	31.786[b]	23.259[a]	24.241[a]	22.925[a]
	CR Dhan 207	30.244[d]	22.283[b]	23.266[b]	22.284[a]
	IR36	29.249[e]	20.292[c]	21.274[c]	20.959[b]
	Kasalath IC459373	30.244[d]	18.261[e]	19.243[e]	18.261[d]
CD(0.05)		**0.070**	**0.093**	**0.093**	**0.739**
Acetone treated	CR Dhan 201	32.203[d]	19.309[d]	20.291[d]	19.643[c]
	CR Dhan 204	33.817[b]	20.292[c]	21.274[c]	20.625[bc]
	CR Dhan 205	33.341[c]	21.351[b]	22.333[b]	21.351[ab]
	CR Dhan 207	39.302[a]	19.309[d]	20.291[d]	19.643[c]
	IR36	29.349[f]	20.302[c]	21.284[c]	20.302[bc]
	Kasalath IC459373	31.230[e]	23.739[a]	24.720[a]	22.739[a]
CD(0.05)		**0.169**	**0.083**	**0.083**	**1.476**
Control	CR Dhan 201	29.199 [a]	17.292 [c]	18.274[c]	17.292
	CR Dhan 204	23.221[d]	18.301[b]	19.283[b]	18.968
	CR Dhan 205	28.198[b]	18.311[b]	19.293[b]	18.644
	CR Dhan 207	26.240[c]	19.310[a]	20.292[a]	19.310
	IR36	21.173[e]	16.914[d]	17.896[d]	18.247
	Kasalath IC459373	29.199[a]	19.309[a]	20.291[a]	19.309
CD(0.05)		**0.167**	**0.05**	**0.05**	**NS**

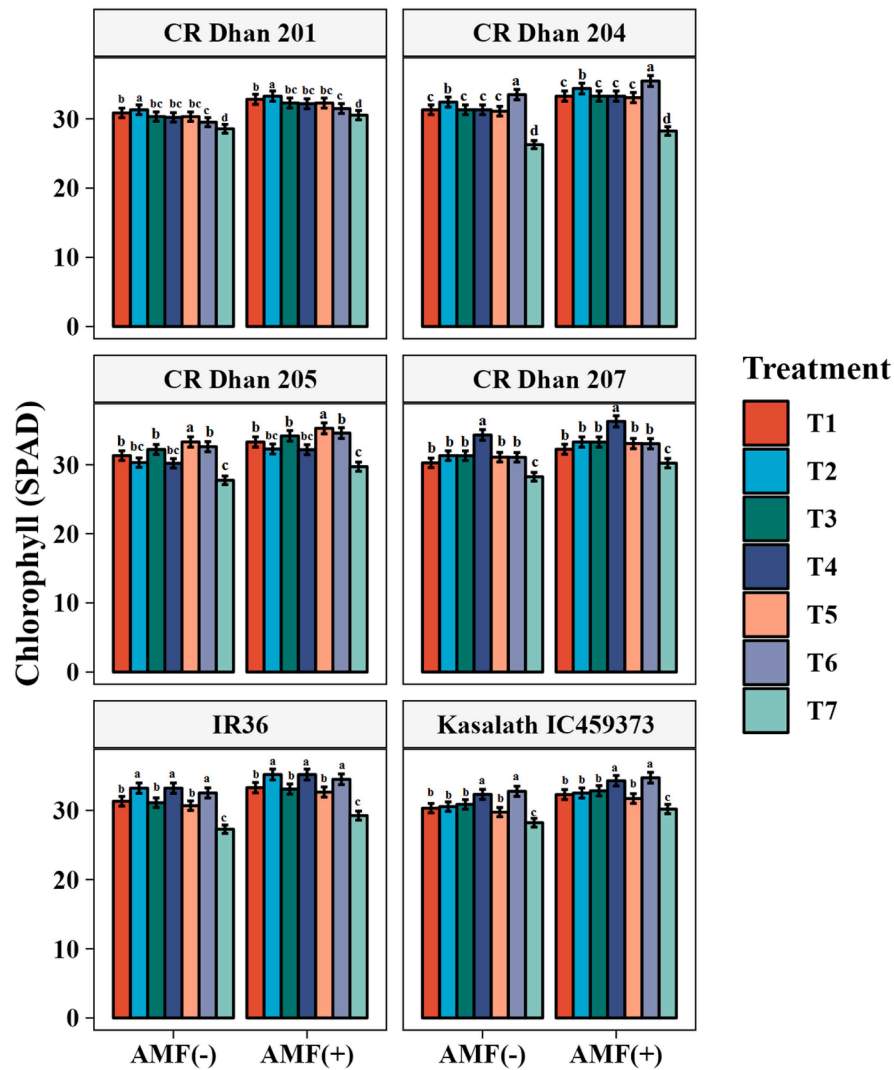Different lowercase letters represent significant variations among the treatment at *p* < 0.05.

Fig. 3. Strigolactone GR24 application effect on chlorophyll (SPAD) in different rice varieties. [T1: 0.1 μM GR24, T2: 0.5 μM GR24, T3: 1.0 μM GR24, T4: 5.0 μM GR24, T5: 10.0 μM GR24, T6: acetone treated, T7: Control, AMF (-): without AMF, AMF (+): with AMF].
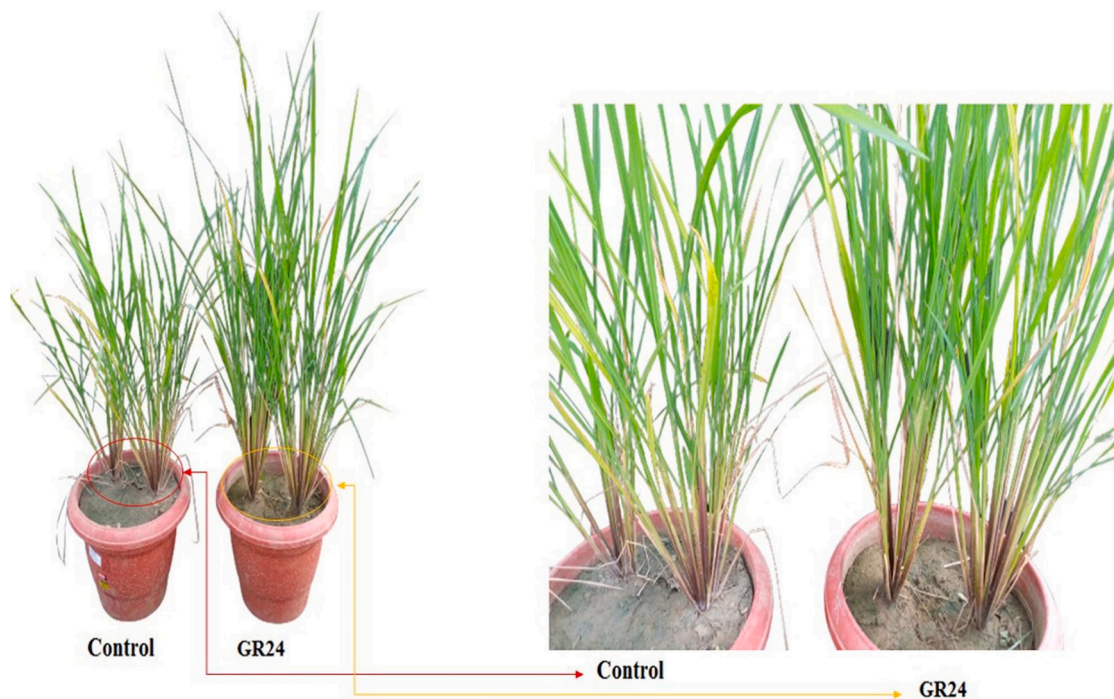
Fig. 4. AMF intervention with GR24 seed priming enhanced rice tiller number under low P accessible soil.

mineralization (Nannipieri et al., 2011), which directly influences the decomposition and transformation of organic phosphate and its bioavailability (Liu et al., 2020). Activity is an indicator of the direction and intensity of soil P biotransformation. Soil phosphatase is influenced by the C, N, and available P content and pH (Wang et al., 2011; DeForest et al., 2012, 2010; Piotrowska-Długosz and Wilczewski, 2014; Hou et al., 2020). This study was conducted to understand how GR24 seed priming, with and without AMF inoculation, affects AcP and AkP activities in different rice varieties under P-deficient conditions. The effects of AcP and AkP activities on GR24 priming, with and without AMF inoculation, varied from variety to variety. However, the activity of AcP showed higher in Kasalath IC459373, CR Dhan 205, CR Dhan 204, and CR Dhan 207 at 0.5, 5.0 and 10.0 µM GR24 priming with AMF inoculation (Table 6; Supplementary Table 1). Kasalath IC459373 treated with 5.0 µM GR24 and AMF showed the highest AkP activity under P-deficient conditions (Table 6; Supplementary Table 1).

3.6. Effect of strigolactone GR24 priming with and without AMF inoculation on chlorophyll (SPAD), tiller number and leaf number in different rice varieties

Strigolactones are a group of phytohormones that play critical roles in plant structures. The effect of SL GR24 application in different crops has been reported by several researchers (Sedaghat et al., 2021; Sun et al., 2022; Ma et al., 2022; Ahsan et al., 2022), however, the interesting work by Yamada et al. (2014) reported the effect of SL-GR24 hormones that inhibit shoot branching and stimulate secondary stem growth, primary root growth, and root hair elongation in P-deficient soil; however, the chlorophyll levels did not differ between the sufficient and deficient phosphate conditions in the wild-type plants, but increased in the SL-deficient mutants, leading to strong promotion of leaf senescence by GR24 treatment. These results suggested that the mutants exhibited increased responsiveness to GR24 under phosphate deficiency. Furthermore, GR24 accelerated leaf senescence in both intact SL-deficient mutants and dark-induced leaf senescence under phosphate deficiency. Similarly, Krasylenko et al. (2021) conducted an experiment

to understand the stimulation of both the SL and karrikin signaling pathways; 3 µM and 25 µM synthetic *rac*-GR24 were used to induce different physiological responses in *Arabidopsis*. The relationship between GR24-dependent inhibition of hypocotyl elongation and changes in cortical microtubule organization and dynamics was discovered in living wild-type and *max2*–1 seedlings that stably expressed genetically encoded fluorescent molecular markers for microtubules. The quantitative evaluation of microscopic datasets revealed that the chemical and/or genetic manipulation of strigolactone signaling impacted microtubule remodeling, especially under light conditions. Interestingly, the application of GR24 in dark conditions partially alleviated cytoskeletal rearrangement, suggesting a new mechanistic connection between cytoskeletal behavior and the light-dependent nature of strigolactone signaling. The analog GR24 (0, 0.5, 1, 2, 4, and 8 µM) has been studied in *Artemisia annua*, and 4 µM GR24 was found to be the most effective in promoting growth, photosynthesis, and other physiological indices (Wani et al., 2023). In another study, four SL GR24 levels (water, 0.001, 0.01, and 0.1 mg L^{-1}) were applied as seed treatment, and the results showed an increase in chlorophyll fluorescence in wheat, and application of GR24 (5 and 10 µM) in *Triticum aestivum* L. *cv*. Sirvan increases photosynthesis and yield under drought stress (Sedaghat et al., 2021). Ali et al. (2021) reported that exposure to penoxsulam (PXL) and bensulfuron-methyl (BSM) significantly reduced cellular damage in both the roots and leaves of watermelon seedlings when GR24 was applied at concentrations of 0, 1, and 5 µM+ half-strength Hoagland solution. In our study, SL GR24 application with AMF in different aerobic rice varieties indicated that seed priming with 5 and 10.0 µM SL GR24 significantly increased chlorophyll (SPAD) and leaf numbers in most of selected aerobic rice varieties (Fig. 3). Fig. 4 shows the application of 5.0 µM GR24 enhanced the tiller number and suppressed outgrowth. 5.0 µM GR24 performed better in CR Dhan 207 for the enhancement of chlorophyll and the highest leaf number in CR Dhan 201, whereas in Kasalath IC459373, a significant improvement in leaf number at 10.0 µM GR24 treatment (Fig. 5).
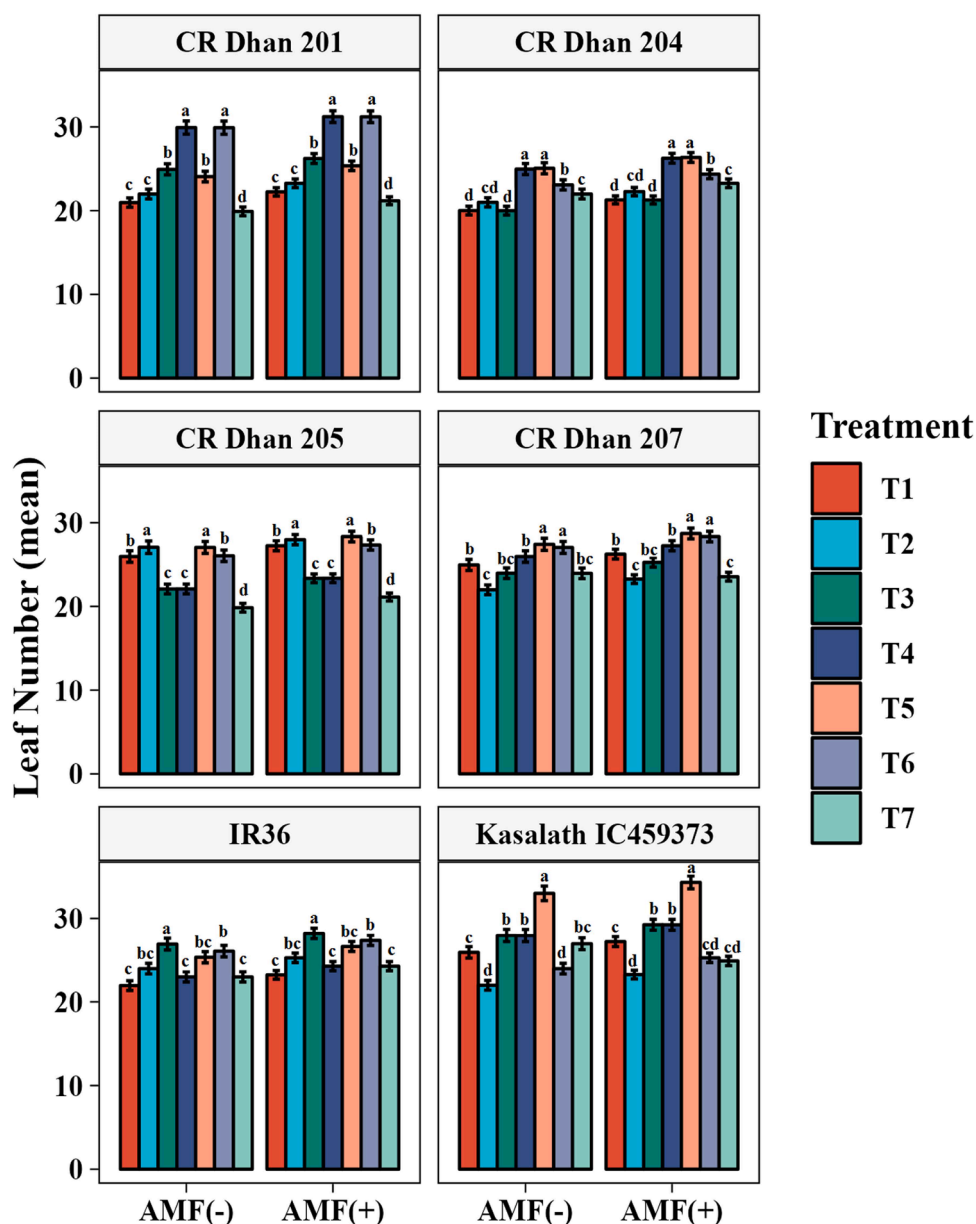
Fig. 5. Strigolactone GR24 application effect on leaf number in different rice varieties. [T1: 0.1 μM GR24, T2: 0.5 μM GR24, T3: 1.0 μM GR24, T4: 5.0 μM GR24, T5: 10.0 μM GR24, T6: acetone treated, T7: Control, AMF (-): without AMF, AMF (+): with AMF].

4. Conclusions

The research aimed to investigate the effects of strigolactone GR24 on plant growth and development using different concentrations of GR24 (0.1, 0.5, 1.0, 5.0, and 10.0 μM) in the presence or absence of arbuscular mycorrhizal fungi (AMF) in selected rice varieties (CR Dhan 201, CR Dhan 204, CR Dhan 205, and CR Dhan 207), Kasalath-IC459373 (P-tolerant check), and IR-36 (P-susceptible check) under P-deficient conditions. Findings of the research showed that priming seeds with 5.0 μM SL GR24 improved the performance of mycorrhization in CR Dhan 205, followed by CR Dhan 204 and 207, and increased the sporulation of AMF in CR Dhan 201, as well as rice growth. AMF treated with 5.0 μM SL GR24, such as CR Dhan 205, followed by CR Dhan 207 and 204, showed the best performance in plant growth, chlorophyll content, and soil functional properties, including acid and alkaline phosphatase activity, soil microbial biomass carbon (MBC), dehydrogenase activity (DHA), and fluorescein diacetate activity (FDA). The AMF intervention with SL GR24 led to a significant increase in plant growth, soil enzyme activity,

and P uptake compared to the control group. In P-deficient conditions, seed priming with 5.0 μM strigolactone GR24 and AMF inoculum significantly enhanced the growth, P uptake, and soil enzyme activities of selected aerobic rice varieties. The application of SL formulations in selected aerobic rice varieties, CR Dhan 207, CR Dhan 204, and CR Dhan 205, can promote mycorrhization and enhance P utilization under P-deficient conditions, leading to improved rice growth.

CRediT authorship contribution statement

D.M., A.S., A.P. and P.P. were involved in the sampling, analysis, visualization and manuscript writing; P.P., P.C. A.K.N. and P.K.D.M. were involved in manuscript refinement, supervision and important intellectual content discussion.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.crmicr.2024.100229.

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