Variations in growth responses of rice varieties to inoculation with plant growth-promoting actinomycete

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Poor overall crop growth during crop establishment when the soil is saturated negatively affects crop performance and adaptation to subsequent drought stress at later growth stages in upland rice-growing environments. *Streptomyces mutabilis*, an actinomycete and a gram-positive filamentous bacterium, can improve growth of rice. This study aimed to determine the potential of *S. mutabilis* in improving crop growth at an early vegetative stage in a rainfed upland condition by quantifying its effect on seed germination, seedling vigor, and root growth. Seeds of each of the irrigated lowland rice varieties such as NSIC Rc 122, NSIC Rc 222, NSIC Rc 240, and NSIC Rc 300 were presoaked in *S. mutabilis* inoculant solution and sown either in moist paper in a Petri dish in the laboratory or in potted water-saturated soil in the greenhouse. The seedling growth and vigor in the Petri dish were assessed at 3 to 7 days after sowing (DAS), while those in the pots at 14 to 28 DAS. In the Petri dish all varieties except NSIC Rc 300 showed greater shoot length, shoot dry weight, and seedling vigor with *S. mutabilis* inoculation relative to their uninoculated counterparts. In the potted water-saturated soil, by contrast, only NSIC Rc 122 and Rc 222 showed greater shoot and root dry weights with *S. mutabilis* inoculation relative to their uninoculated counterparts. Under *S. mutabilis* inoculation, NSIC Rc 300 had less growth than the other three varieties in both Petri dish and potted water-saturated soil possibly due to rice-actinomycete symbiosis. The results indicate that the response to *S. mutabilis* inoculation was variety dependent, and thusthis observed genetic variations in response to inoculation can be utilized in breeding. Further studies under a moisture condition controlled by polyethylene glycol (PEG) in a Petri dish and under a different magnitude of upland soil moisture conditions are needed to validate the effect on growth performance as well as yield response. Also, the symbiotic relationship between the rice variety and actinomycete inoculations needs to be further explored.

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INTRODUCTION

Rice production in upland areas generally suffers from drought stress due to its dependency on water from rainfall, which is becoming erratic due to the effect of climate change. In fact, the current upland rice yield in the Philippines is low at approximately 2 t ha^{-1} due partly to the uncertainties of rainfall patterns (Cruz et al. 2015; Mohanty et al. 2013).

While advances in agriculture to mitigate the effect of abiotic stress contributed to the increase in crop yields (Harris 2004),

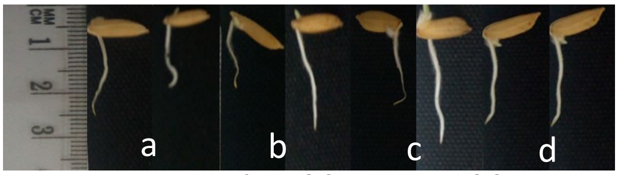


Figure 1: Root lengths of (a) NSIC Rc 122, (b) NSIC Rc 222, (c) NSIC Rc 240, and (d) NSIC Rc 300 at 3 days after sowing as affected by *S. mutabilis* inoculation during seed soaking prior to germination. Note: left-uninoculated, right-inoculated.

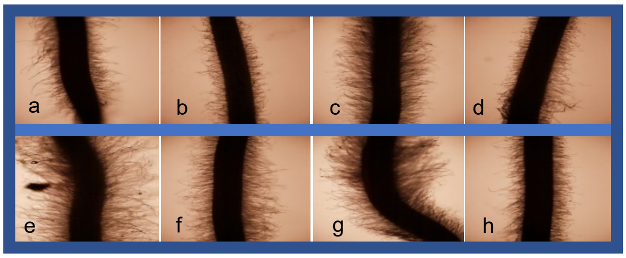


Figure 2: Root hair development of NSIC Rc 122 (a,e), NSIC Rc 222 (b,f), NSIC Rc 240 (c,g), and NSIC Rc 300 (d,h) at 3 days after sowing in Petri dish under uninoculated (a-d) and inoculated (e-h) treatments. Note: *S. mutabilis* inoculants were applied during seed soaking prior to germination (magnification: 400x).

such advances are better suited only in developed countries where there are substantial financial investments in machinery, chemical fertilizers, and crop protection compounds. In contrast, in developing countries, there is a need to find an economically feasible alternative that can cater to the needs of mostly marginal rice farmers in high-risk upland environments (Harris 2004).

Thus, improving poor crop establishment at a minimal cost before the occurrence of drought to increase yield and net income in upland rice areas can be one of the alternatives.

Drought is particularly frequent in unbunded uplands, bunded uplands, and shallow rainfed lowland fields planted to rice. In the upland rice areas, soil water content frequently falls to field capacity or below in the root zone (Serraj et al. 2011) especially during the late vegetative and reproductive stages of plant growth (Boling et al. 2004; Heinemann et al. 2015; Gabiri et al. 2018). Drought mitigation through improved root system and/or improved agronomic practices (Suralta et al. 2018) is key to maintaining yield in these areas. Upland rice is established via direct seeding normally during the onset of the wet season. Seed germination proceeds when the soil is wet and saturated after the start of the rainy season and usually the soil remains saturated for about a month coinciding with the early vegetative stage of rice growth (Boling et al. 2004; Heinemann et al. 2015; Gabiri et al. 2018). Thus, rapid seed germination and uniform seedling vigor to attain optimum crop establishment (Sawan et al. 2011) and extensive root system prior to the occurrence of drought during the late vegetative and reproductive stages of growth (Boling et al. 2004; Heinemann et al. 2015; Gabiri et al. 2018) can contribute positively to the subsequent expression and adaptive root traits and water extraction during water stress (Kamoshita et al. 2002) and consequently maintain a high yield potential. One way to achieve this is through agronomic management such as the use of plant growth-promoting bacteria (Suralta et al. 2018).

Plant growth-promoting bacteria (PGPB) as biofertilizers are an important part of the integrated plant nutrient management systems, particularly in rainfed areas, where farmers normally rely on either “no-cost” or “low-cost” inputs (Desai et al., 2016). PGPB are microorganisms that can grow in, on, or around plant tissues and stimulate plant growth through various mechanisms including but not limited to nitrogen fixation, phosphate solubilization, iron sequestration, modulation of phytohormone levels, indole-3-acetic acid (IAA) and 1-aminocyclopropane-1-carboxylate (ACC)-deaminase, and siderophore production (Vessey 2003; Glick 2012). Due to their growth and productivity promoting potential in plants, a wide-reaching effort in the agro-industry sectors to search a viable microorganism has surged in recent years including actinomycetes as a source of agro-active compounds and of biocontrol tools (Behal 2000; Tanaka and Omura 1993).

Actinomycetes, a gram-positive aerobic bacterium showing a fungi-like filamentous growth (Jeffrey 2008), are one of the major components of the microbial populations in soil interacting with higher plants in various ways (Franco-Correa et al. 2010; Muthu et al. 2013). Recently these filamentous bacteria have found their new niche in agriculture as potential PGPB due to their ability to produce IAA, ACC-deaminase, siderophore, and solubilize phosphate *in vitro* (Cruz et al. 2014), which in specific cases trigger faster seed germination (Mia et al. 2012), improved drought tolerance ability (Suralta et al. 2018), or act as a natural plant growth hormone, controlling many development processes (Patil and Patil 2012).

Recently an actinomycete was isolated from Binangonan soil in Rizal, Philippines, with probable identity as *Streptomyces mutabilis* with 98% of maximum identity based on 16S rDNA analysis (Cruz et al. 2015). *Streptomyces mutabilis* produced plant growth-promoting compounds such as ACC deaminase, Indole-3-acetic acid and phosphatase either of which was responsible for promoting rice growth under laboratory room conditions (Cruz et al. 2014, 2015). In this study, we hypothesized that a *Streptomyces mutabilis* could improve seed germination and seedling growth in rice, which are important factors for improving crop establishment and extensive root system development during the early vegetative stage when the soil is still at saturated conditions. We specifically explored responses of irrigated lowland rice varieties to *S. mutabilis* inoculations because of their higher yield potential than the rainfed lowland and upland rice varieties (Liu et al. 2019; Saito et al. 2015) which can be harnessed in rainfed areas normally experiencing late vegetative and reproductive stage drought conditions. Thus, this study evaluated the effectiveness of *S. mutabilis* inoculation on the germination and early seedling shoot and root growth at early vegetative stages of four irrigated lowland rice varieties (NSIC Rc 122, NSIC Rc 222, NSIC Rc 240, and NSIC Rc 300) under laboratory and screenhouse conditions.

MATERIALS AND METHODS

Time and place of study

Two experiments were conducted: one each under laboratory and screenhouse conditions at the Agronomy, Soils, and Plant Physiology Division, Philippine Rice Research Institute - Central Experiment Station (PhilRice-CES), Muñoz, Nueva Ecija, Philippines (15° 40’ N, 120° 53’ E, and 57.6 MASL).

Preparation of actinomycete inoculant

The *S. mutabilis* culture was obtained from the Agronomy, Soils and Plant Physiology Division (ASPPD), Philippine Rice Research Institute. This bacterium was maintained on arginine-glycerol-salt (AGS) agar slants.

A soil-based carrier was used for inoculant preparation. For the preparation of a soil-based carrier, components (soil and charcoal) were pulverized, sieved, and mixed at a ratio of 3 soil : 1 charcoal and sterilized in an autoclave at 121°C for 1 hour a day for 3 consecutive days. *S. mutabilis* culture was grown in AGS broth for 7 days under room temperature. Twenty-two ml

Table 1: Shoot and root lengths, shoot dry weight, and seedling vigor of NSIC Rc 122, Rc 222, Rc 240, and Rc 300 as affected by actinomycete inoculation at 7 days after sowing in Petri dish.

Rice Varieties	Treatment	Shoot length (cm plant^{-1})	Root length (cm plant^{-1})	Shoot dry weight (mg plant^{-1})	Seedling vigor
NSIC Rc 122	Uninoculated	1.92	3.07	2.03	18.34
	Inoculated	4.77*	5.58^{ns}	6.17*	38.09*
NSIC Rc 222	Uninoculated	1.58	0.92	1.33	9.20
	Inoculated	3.97*	7.43*	5.03*	41.95*
NSIC Rc 240	Uninoculated	2.78	2.97	3.33	21.16
	Inoculated	5.22*	7.23*	7.23*	49.80*
NSIC Rc 300	Uninoculated	3.00	4.92	3.87	31.67
	Inoculated	4.47^{ns}	6.48^{ns}	5.10^{ns}	43.80^{ns}

ns- not significant; *- significantly different between inoculation treatments within each variety, at 5% least significant difference.

Table 2: Shoot and root dry weights, and number of tiller per plant of different irrigated lowland rice varieties as affected by actinomycete inoculation at 28 days after sowing in soil.

Rice Varieties	Treatment	Shoot dry weight (g plant^{-1})	Root dry weight (g plant^{-1})	Tiller (no. plant^{-1})
NSIC Rc 122	Uninoculated	1.20	0.35	4.0
	Inoculated	2.47*	0.70*	6.0^{ns}
NSIC Rc 222	Uninoculated	0.57	0.20	3.0
	Inoculated	1.90*	0.73*	6.0*
NSIC Rc 240	Uninoculated	1.53	0.40	4.0
	Inoculated	2.10^{ns}	0.53^{ns}	5.0^{ns}
NSIC Rc 300	Uninoculated	1.63	0.53	6.0
	Inoculated	2.10^{ns}	0.77^{ns}	5.0^{ns}

ns- not significant; *- significantly different between inoculation treatments within each variety, at 5% least significant difference.

of *S. mutabilis* culture broth was aseptically transferred to 100 g of sterilized soil-based carrier and incubated for 7 days.

Rice varieties used

Four randomly selected irrigated lowland rice varieties (NSIC Rc 122, NSIC Rc 222, NSIC Rc 240, and NSIC Rc 300) were used in both experiments. These varieties had yield potential above 6 t ha^{-1} under irrigated lowland conditions.

Experiment 1. Effectiveness of *S. mutabilis* inoculation on early shoot and root development and seedling vigor of rice under laboratory conditions

In the laboratory, two treatments were imposed: uninoculated (control) and inoculated treatments. In uninoculated control, the surface-sterilized seeds were presoaked in distilled water for 30 min. In inoculated treatment, by contrast5 g of *S. mutabilis* inoculant was dissolved in 100 ml sterilized distilled water and used for the presoaking of seeds for 30 min. Twenty-five seeds of each of the 4 irrigated lowland varieties presoaked in water either uninoculated or inoculated with *S. mutabilis* were sown in moist filter paper in a Petri dish and replicated 3 times. The presoaked seeds in all treatments were incubated and grown at room temperature.

The number of germinated seeds was counted starting at 3 days after sowing (DAS). The seeds were considered germinated when radicle was ≥ 2mm. The seed germination rate was calculated as the ratio of the number of germinated seeds to that of the total number of seeds expressed as a percentage.

Similarly, root hair development was examined at 3 DAS by cutting a 1-cm segment from the seminal root and observed under a system microscope (Olympus CX41, Olympus Corporation, Tokyo, Japan) at 400x magnification. Digitized images were taken from a camera attached to the microscope.

At 7 DAS, root and shoot lengths of each seedling were measured to determine the vigor index computed as the ratio of the sum of the lengths of root and shoot to that of the total number of seed multiplied by percent germination (Abdul Baki and Anderson 1973).

Experiment 2. Effectiveness of *S. mutabilis* inoculation on the seedling growth and development of rice in well-saturated soil under screenhouse conditions

In the screenhouse we also evaluated the effectiveness of *S. mutabilis* inoculation on the seedling growth and development of rice in a well-saturated soil. Two treatments were imposed: uninoculated (control) and inoculated treatments. In uninoculated treatments, the surface-sterilized seeds of each variety were presoaked in distilled water for 30 min. In inoculated treatments, by contrast surface-sterilized seeds were presoaked in *S. mutabilis* inoculant suspension for 30 min. The surface-sterilized seeds were sown in plastic pots (Magenta jars) containing air-dried and sieved soil (Maligaya clay loam) previously sterilized in an autoclave for 1 h a day at 121°C for 3 consecutive days. Sterilized Simple Nutrient Addition Program (SNAP) solution was used as a nutrient source.

Plant height was measured using a meterstick, while the number of tillers was manually counted at 14, 21, and 28 DAS. At 28 DAS the experiment was terminated. The shoots from each pot were cut, oven dried at 70^{O}C for 3 days prior to weighing of the dry weight. The roots from each pot were also extracted and cleaned with running water. The root samples were oven dried at 70^{O}C for 3 days prior to weighing of the dry weight.

Statistical analysis

A split-plot design, the main plots arranged in a randomized complete block with three replications was used for both experiments. Varieties were assigned as main plots and the inoculation treatments as subplots. The data from both experiments were subjected to two-way ANOVA using SAS 9.1.3. The means were compared by the least significant difference (LSD) at the 0.05 probability level.

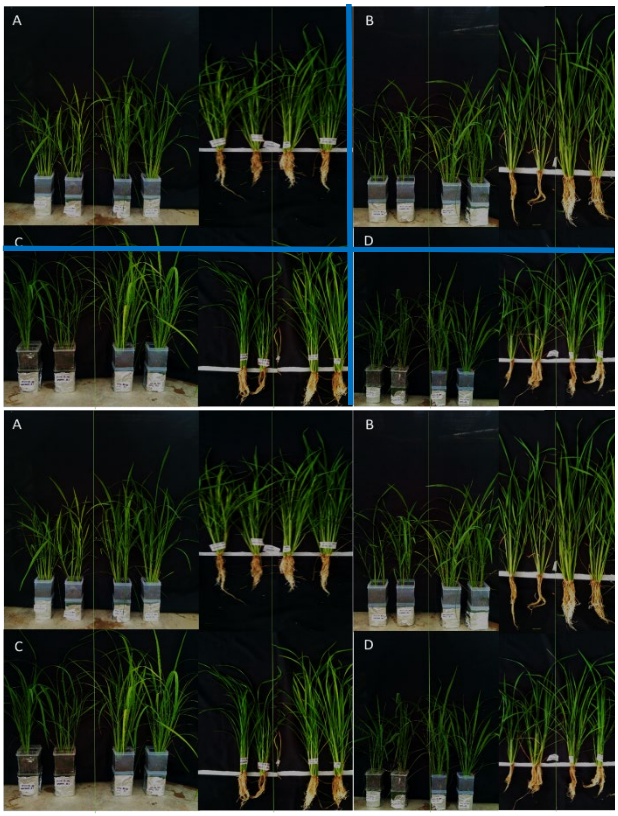


Figure 3: Rice seedlings of (a) NSIC Rc 122, (b) NSIC Rc 222, (c) NSIC Rc 240, and (d) NSIC Rc 300 as affected by *S. mutabilis* inoculation at 28 days after sowing in potted water-saturated soil conditions. Note: left-uninoculated, right-inoculated

RESULTS AND DISCUSSION

Experiment 1. Effectiveness of *S. mutabilis* inoculation on early shoot and root development and seedling vigor of rice seedlings under laboratory conditions

The effects of *S. mutabilis* inoculation on root elongation and root hair development of different irrigated lowland rice varieties are presented in figures 1 and 2, respectively. Visually, inoculation of seeds with *S. mutabilis* generally promoted root hair development of NSIC Rc 122 and NSIC Rc 222 at 3 DAS, relative to their uninoculated counterparts. Root length in NSIC Rc 240 also increased 38% under *S. mutabilis* inoculated relative to uninoculated control at 3 DAS. Increased root growth caused by *S. mutabilis* inoculation may provide seedlings a greater opportunity for water absorption before moisture loss occurs in soil especially under field conditions.

At 7 DAS, *S. mutabilis* inoculation significantly increased the shoot length of NSIC Rc 122, NSIC Rc 222, and NSIC Rc 240 by 148, 151, and 88%, respectively, relative to their uninoculated counterparts. The root length was also significantly increased by 708 and 143% in NSIC Rc 222 and NSIC Rc 240 under *S. mutabilis* inoculation. The shoot dry weight of NSIC Rc 122, NSIC Rc 222, and NSIC Rc 240 significantly increased by 204, 278, and 117%, respectively, under *S. mutabilis* inoculation (table 1). The significant improvement on the shoot and root growth and development of rice seedlings with *S. mutabilis* inoculation was potentially caused by the production of bacterial IAA (table 1; Cruz et al. 2014). IAA is a class of auxin that can promote the formation and elongation of roots and root hairs, and the initiation and emergence of lateral roots (Aziz et al. 2015).

Seedling vigor was generally improved by *S. mutabilis* inoculation of most of the varieties by 108 to 356% except NSIC Rc 300. The production of IAA by an actinomycete increased the synthesis of auxin, consequently increasing seedling vigor previously reported in maize (Venkatachalam et al. 2010), wheat (Doolotkeldieva et al. 2015; Yandigeri et al. 2012) and soybean (Doolotkeldieva et al. 2015) inoculated with various species of actinomycetes. Actinomycete inoculation also improved rice crop establishment through an enhanced seedling vigor (Mia et al. 2012). High vigor seeds are prerequisite for better establishment of seedling in the field (Mia et al. 2012) as more vigorous rice seedlings had a better chance of surviving drought under rainfed growing areas.

Supplementary Table 1: Plant height of different rice varieties as affected by *S. mutabilis* inoculation at 14, 21, and 28 days after sowing in potted water-saturated soil conditions.

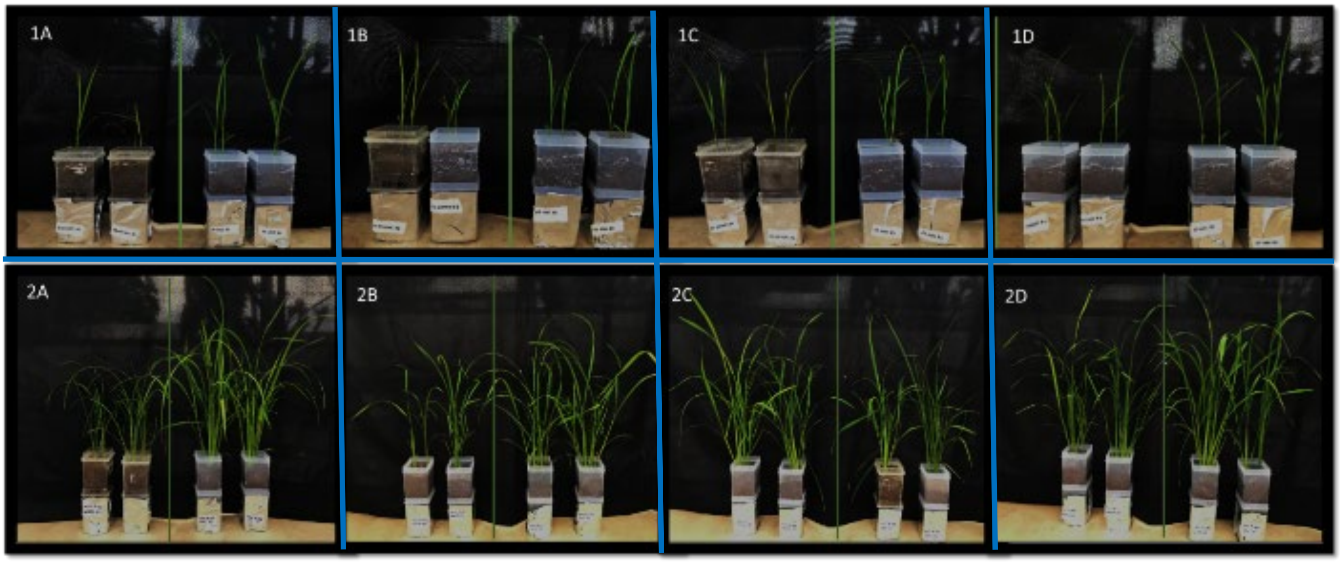
Variety	Treatment	Plant height (cm)		
		14 DAS	21 DAS	28 DAS
NSIC Rc 122	Uninoculated	20.7	30.3	50.1
	Inoculated	36.3*	48.7*	55.4^{ns}
NSIC Rc 222	Uninoculated	16.3	27.1	47.0
	Inoculated	27.7^{ns}	41.1*	52.1^{ns}
NSIC Rc 240	Uninoculated	23.8	36.8	48.7
	Inoculated	27.7^{ns}	42.8^{ns}	54.1^{ns}
NSIC Rc 300	Uninoculated	28.3	41.1	51.0
	Inoculated	33.6^{ns}	44.3^{ns}	52.4^{ns}

ns, not significantly different between inoculation treatments; *significantly different at 5% least significant difference.

Experiment 2. Effectiveness of *S. mutabilis* inoculation on the seedling growth and development of rice in well-saturated soil under screenhouse conditions

The overall plant stature (shoot and root system) of the four irrigated lowland rice varieties under two inoculation treatments and grown under well-saturated soil conditions for 28 DAS is presented in figure 3. The ANOVA revealed a significant interaction between variety and *S. mutabilis* inoculation treatments on shoot dry weight, tiller number, and root dry weight at 28 DAS. Specifically, shoot and root dry weights were generally increased by *S. mutabilis* inoculation but such increases were significant only in NSIC Rc 122 and NSIC Rc 222 (table 2). Taller plants were generally observed under *S. mutabilis* inoculations regardless of varieties at 28 DAS, although such differences were not significantly different from their uninoculated counterparts (supplementary table 1). During the early stage of growth, plant height was significantly increased by *S. mutabilis* inoculation in some of the varieties such as in NSIC Rc 122 at 14 and 21 DAS, and NSIC Rc 222 at 21 DAS only (supplementary table 1). The tillering ability was not significantly affected by *S. mutabilis* inoculation in most varieties except NSIC Rc 222 where tillering was doubled under inoculation (table 2).

IAA stimulates root tissue development and thus increases the size of the root system and its capacity to take up water and nutrients required for aboveground plant function (Tate III 2000; Suralta et al. 2018). A wide variety of microorganisms are known to produce plant growth hormones such as IAA. In tomato, actinomycete inoculation increased IAA production and subsequently increased its growth (El-Tarabily 2006). In rice, inoculation with PGPB increased soil nitrogen uptake, shoot growth and grain yield (Rasul 1999), and drought tolerance (Suralta et al. 2018). The positive effects of PGPB on plant growth especially under drought-prone growing conditions were triggered by phytohormones and enzymes produced by the bacteria consequently contributing to greater promotion in lateral root development as well as in the production of root hairs and thus resulting in a greater root system ideal for supporting greater plant growth and development (Suralta et al. 2018).



Supplementary Figure 1: Rice seedlings of (A) NSIC Rc 122, (B) NSIC Rc 222, (C) NSIC Rc 240, and (D) NSIC Rc 300 as affected by S. mutabilis inoculation at 14 (1A-1D) and at 21 (2A-2D) days after sowing in potted water-saturated soil conditions. Note: left-uninoculated, right-inoculated.

Although variety by *S. mutabilis* inoculation interactions exists on most agronomic parameters, increased seedling growth due to rhizobacteria on seedlings of sugar beets (Dunne et al. 1998), soybean (Cattelan et al. 1998) and rice (Nandakumar et al. 2001; Ashrafuzzaman et al. 2009; Beneduzi et al. 2008), but not generally with synthetic growth-promoting chemicals (Nandakumar et al. 2001). In some cases, an increase in plant height contributed to the increase in yield in some crops (Pierson and Weller 1994; Duffy and Weller 1995). In the present study and with the current findings, what is important is to quantify further quantify the effect of *S. mutabilis* inoculation on the final yield of different rice varieties under drought-prone soil conditions. This will provide an empirical evidence towards the development of biofertilizers containing *S. mutabilis.*

The current findings also suggest a significant genotypic variation in the response of rice growth and development to *S. mutabilis* inoculations. Hence, genetic variations in terms of the response in yield performance to *S. mutabilis* inoculations including the physiological basis need to be further validated. The information generated will be useful in breeding rice for an improved response to actinomycete inoculations.

CONCLUSION

In the laboratory, inoculation of rice seeds with *S. mutabilis* improved the root hair development in NSIC Rc 122 and Rc 222 seedlings as early as 3 days DAS. It also significantly increased shoot length, shoot dry weight, and seedling vigor of all varieties used at 7 DAS.

In the screenhouse, there was a significant interaction between variety and *S. mutabilis* inoculation treatments on shoot dry weight, tiller number, and root dry weight at 28 DAS. Specifically, shoot and root dry weight were consistently increased by inoculation treatments, but such increases were significant only in NSIC Rc 122 and NSIC Rc 222. This indicates that *S. mutabilis* inoculation can improve the growth of irrigated lowland varieties and make them perform well under well-saturated soil, although this is variety dependent.

Overall, the results implied that *S. mutabilis* can be a potential bioinoculant for a specific set irrigated lowland rice. The significant improvement in seedling vigor, and shoot and root growth and development, due to *S. mutabilis* inoculant was evident in NSIC Rc 122 and NSIC Rc 222. Further studies will be conducted to evaluate whether these initial findings would translate to the maintenance of a higher yield of these irrigated rice varieties together with other selected rainfed lowland and upland varieties under upland growing conditions of drought stress starting at a late vegetative stage of growth.

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