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SALICYLIC ACID SIGNALING AND BACTERIAL ROOT COLONIZATION IN RICE

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ABSTRACT

Salicylic acid (SA), a plant defence hormone, is one of the compounds present in the root exudates. It helps in organization of root microbiome of the plant. The present study was undertaken to correlate SA content with bacterial root colonization in widely cultivated Asian rice varieties, Parmal/Non-Basmati (PR121, PR122 and PR126) and Basmati varieties (Punjab Basmati number 3- Pb Bas-3; Punjab Basmati number 5- Pb Bas 5and Pusa Basmati- PusaBas 1121) and a wild variety (Labra). Standard microbiological procedures were used for bacterial isolation on various selective media for enumeration of total viable count, count of spore formers, free-living nitrogen fixers, symbiotic nitrogen fixers, Gram negative and Gram positive bacteria. Salicylic acid was estimated using High Performance Liquid Chromatography (HPLC). Results revealed that the root endophytic population establishes itself between 60 and 90 days after transplant (DAT). Increase in SA content, from time of transplant to 60 DAT, was commensurate with bacterial invasion of root tissue. Decrease in SA concentration at 90 DAT facilitated the rice root colonization. Persistence of SA throughout the cultivation time period kept the defense system at high alert. No disease was encountered throughout the cultivation time period of this study.

Keywords: Asian rice varieties, Basmati, Parmal/Non-Basmati, Root microbiome, Salicylic acid

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The world population is expected to exceed 9.7 billion by 2050 (Gu *et al*., 2021; Hu *et al*., 2022). Growing population presents many socio-economic challenges. The gravest challenge perhaps, is that of meeting food security needs of the world population. According to FAO, world production of primary crops, wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*), and soy-beans (*Glycine max*), in 2021 was 4 billion metric tons. It must increase by 2.4% per year to keep pace with the increasing population. However, these primary food crops are growing at only half of this required rate (Tian *et al.,* 2021). Agricultural productivity and sustainability can be improved by scientific breakthroughs and technological innovations. These include next generation plant breeding strategies based on genome editing, improving nutritional quality of crops by metabolic engineering, plant and rhizospheric microbiome engineering, increasing efficiency of use of agricultural resources, etc. (Hu *et al*., 2022; Gao, 2021). Engineering of plant endophytic microbiome and rhizospheric microbiome are environment friendly and economical approaches which involve use of microbial strains for enhanced nutrient utilization and developing plant resistance to biotic and abiotic stresses.

Rice (*Oryza sativa*) is one of the main staple crops in world with nearly 2.5 billion people depending on it for food. Globally, it is cultivated in more than 164 million hectares (Brar and Khush, 2013). Rice production is gaining importance in context of high population growth especially in developing countries who are major producers as well as major consumers (Hussain *et al*., 2020; Sanchez *et al.,* 2013). Rice is important cereal also because it provides 21% of per capita energy per person and 15% per capita protein per person which is highest among cereal crops (Sethy *et al.,* 2021).

Plant and soil associated microbial communities are an outcome of plant-microbe interactions. Plant metabolites, secreted into the soil as root exudates facilitate the selection of microbes from the host rhizospheric soil and colonization of the plant by them (Waldor *et al*., 2015; Dastogeer *et al*., 2020). Rhizospheric microbes are selected by chemo-attraction towards carbon compounds present in plant root exudates. These compounds include sugars, amino acids, phenolic compounds, flavonoids, etc (Badri *et al.,* 2009). The microbiota both plant and soil assist the plant in adaptation to adverse environment by mitigating the effect biotic and abiotic stresses (Bhattacharyya *et al*., 2015; Bhattacharyya and Lee, 2016; Jansson and Hofmockel, 2020). They promote plant growth by competing with pathogens for nutrients and space, produce siderophores and induce plant resistance (Santoyo *et al*., 2016; Afzal *et al.,* 2019). Consequently, unraveling the role of root exudates and their composition is essential for engineering endophytic and rhizospheric ecosystem for enhancing plant productivity.

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A constituent of root exudates, Salicylic acid (SA), is reported to define the qualitative and quantitative nature of root microbiome and also microbial dynamics in root rhizospheric soil (Lebeis *et al.,* 2015). It is a plant phenolic compound (Gacnik *et al.,* 2021) which acts as a stress messenger and induces hypersensitive response in plant to screen permeating organisms. It also plays a role in colonization of internal plant tissue. In the present study, attempt was made to correlate SA content and bacterial root colonization at different stages of growth of popularly cultivated Asian rice varieties- Parmal varieties and Basmati varieties and a wild variety. Our hypothesis was that root tissue is rapidly colonized in reduced amount of SA. The hypothesis was tested by estimating differential microbial counts and SA content in rice roots at different stages of growth. The rice seedlings were generated *in vitro* by tissue culture methods to focalize on microbes selected from rhizospheric soil. In addition, plant growth and yield attributes were recorded at the time of harvest. Related work has been reported in *Arabidopsis thaliana* but information on traditionally cultivated Asian rice varieties is short of.

MATERIALS AND METHODS

The present work was carried out in the research laboratories of Department of Microbiology and School of Agricultural Biotechnology, Punjab Agricultural University Ludhiana and in the School of Public Health and Zoonosis, Guru Angad Dev Veterinary and Animal Sciences University Ludhiana. The rice varieties which were part of this investigation are Parmal/Non-Basmati varieties (PR121, PR122 and PR126) and Basmati varieties (Punjab Basmati-3, Punjab Basmati-5, and Pusa Basmati 1121). The behavior of these cultivated varieties was compared with a wild variety (Labra) to gain perspective.

Preparation of tissue culture generated seedlings

Tissue culture generated seedlings were prepared for isolation of only putative endophytes recruited from the rhizospheric soil and disregard any other source of entry of microbes into roots. It was performed in the laboratory facility at School of Agricultural Biotechnology, Punjab Agricultural University Ludhiana.

Preparation and sterilization of growing medium

Murashige Skoog (MS) medium was used for generation of rice seedlings. Five stock solutions of MS media were prepared. The stock solutions were prepared as per Mineo (1990). 50 ml of stock solution 1, 20 ml of stock solutions 2 and 3, respectively and 10 ml of stock solutions 4 and 5, respectively, were mixed. 30 g of sucrose, 100 mg of Myoinositol and 3.55 g of supplement were added to the mixtures of stock solutions. The mixture was stirred continuously as components were being added. The pH was adjusted to

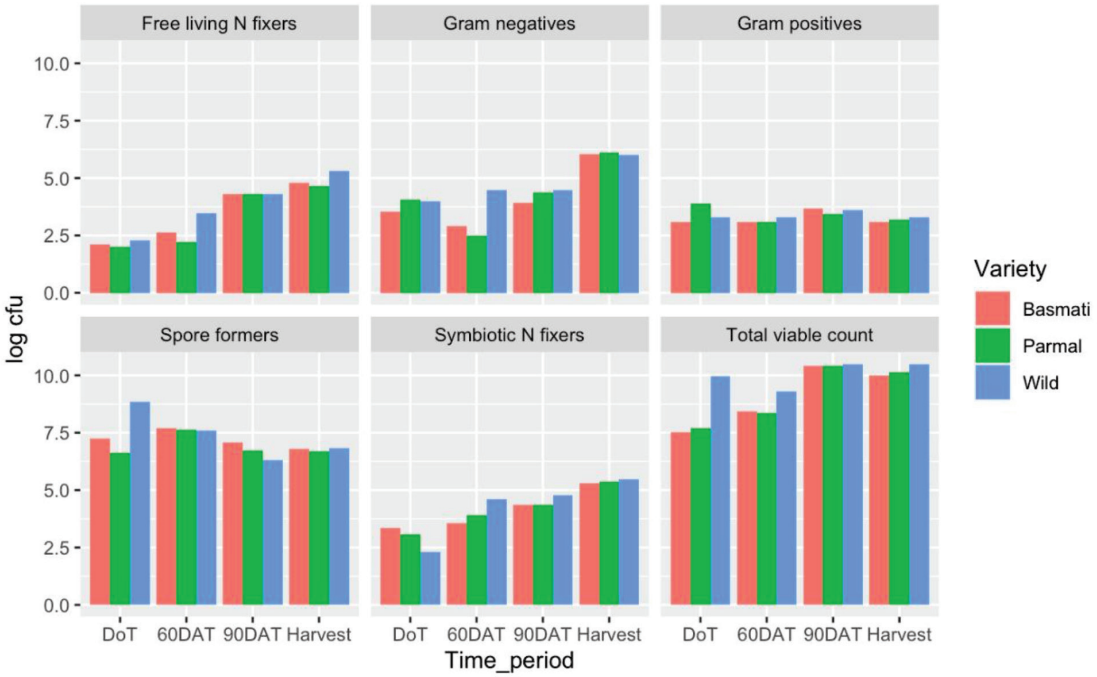


Fig. 1. Microfloral profiling of root tissue of Basmati and Parmal varieties of rice (DoT- day of transplant, 60 DAT- 60 days after transplant, 90 DAT- 90 days after transplant and time of harvest)

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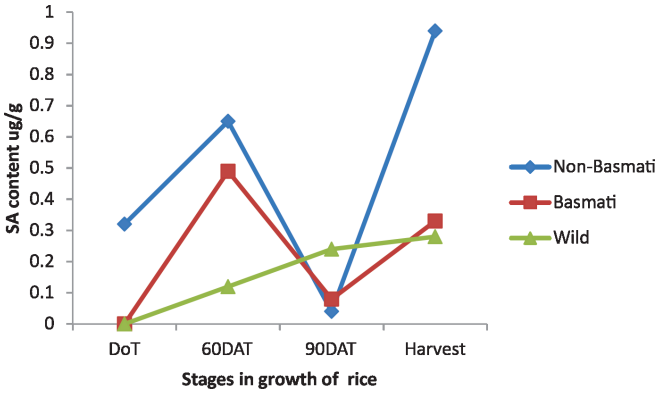


Fig. 2. Salicylic acid concentration in roots of Parmal/ Non- Basmati, Basmati and wild varieties of rice at different stages of growth

5.2±0.6 using 1M NaOH or 1M HCl. Distilled water was added to make the total volume upto 1 litre. 10 g of agar weighed out and added to the MS solution. The solution was heated gently with stirring. This warm medium was poured into the sterilized test tubes and tubes were autoclaved at 15 psi for 15 minutes.

Seedling preparation

Grains of rice plant were used as explants for seedling preparation. They were treated with Bavistin for 10 minutes to prevent fungal contamination. Surface sterilization was done using 0.1% mercuric chloride for 1-2 minutes inside the laminar cabinet. Seeds were then thoroughly washed with 70% ethanol and distilled water. They were inoculated aseptically in test tubes containing MS medium. After inoculation the test tubes were incubated at 25±2°C, providing at least 12 hours of light per day for 10-15 days. Hardening was performed after emergence of seedlings. Seedlings were taken out from the test tubes, washed with water for complete removal of MS medium. They were then kept on wet cotton in a beaker for 2-4 days at temperature 25±2°C. After hardening the seedlings were transplanted in the field.

Field experiment

The experiment was laid out in the Students` Research Fields of the School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana. 20 day old tissue culture generated seedlings of rice varieties were transplanted in the field. There were total 350 plants (50 plants of each variety). The crop was harvested at physiological maturity of rice varieties. This field trial was conducted using Randomized Complete Block Design (RCBD) with three replications of each variety. Total number of blocks were 21, for seven rice varieties. Agricultural practices recommended by Punjab Agricultural University, Ludhiana were complied with during the cultivation time period.

Microfloral profiling of root endophytes

Microbial profiling of endophytes of the root tissue was done at different stages in the growth of rice- vegetative growth, reproductive and maturation/ripening stage. These were- at the time of transplant (DoT), 60 days after transplant (60 DAT), 90 days after transplant (90 DAT) and at the time of harvest. Uprooted roots were patted to remove extra soil and washed with sterile water many times for complete removal of soil. They were then surface sterilized with 0.1 % mercuric chloride solution for 1-2 minutes followed by thorough washing with 70% ethanol and distilled water. Ten grams (fresh weight basis) roots were macerated in sterile pestle mortar under aseptic conditions. The contents were transferred to a sterile flask containing sterile phosphate buffer saline (PBS) pH 7.0.It was then sonicated using 3 mm sonication probe with output frequency 20 kHz, power 200 W, amplitude: 310 µm (Bandelin Sonopuls HD2200 equipped with MS73). Tubes containing roots were cooled (4°C) during sonication steps to prevent heat damage to root tissue and microbial cells. The sonicated suspensions containing microbial cells and root tissue debris were filtered through Whatmann filter paper of 10 µm pore size. The filtered suspension was serially diluted and plated on selective microbiological medium- Nutrient agar for total microbial count, Yeast Extract Mannitol agar for count of symbiotic nitrogen fixers, Jensen`s agar for count of free living nitrogen fixers, MacConkey's agar for count of Gram negatives and Mannitol Salt agar for count of Gram positives. The poured petri plates were incubated at 28±2°C for 48-72 h. The colony count was recorded.

Estimation of salicylic acid (SA)

Salicylic acid present in the root tissue was estimated in the School of Public Health and Zoonosis, Guru Angad Dev Veterinary and Animal Sciences University Ludhiana. HPLC was performed on root tissue samples drawn at the time of transplant, 60DAT, 90DAT and at the time of harvest. Sample preparation for Salicylic acid was done as per the method of Toiu *et al.* (2011). Two grams of rice root tissue was pulverized in sterile pestle mortar to a powdered form. 70% ethanol and 2 ml of 2 M HCl was added to it. It was kept at 80°C on water bath for extraction. It was then centrifuged at 4000 rpm to separate the solid contents. The solution was evaporated in a vacuum evaporator until all liquid had evaporated. 1 ml of the mobile phase was added to the remaining residue. Agilent 1260 infinity II HPLC Series equipped with a Merck C18 reversed-phase analytical column 250 mm x 4.0 mm (i.d.5 µm particle) operated at 45°C was used for estimation of SA. The mobile phase was binary gradient- distilled water with 0.1%

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Table 1. Plant growth and yield parameters in different rice varieties at harvest stage.

S. No.	Parameter	PR121	PR122	PR126	Pb Bas-3	Pb Bas-5	Pusa Bas-1211	Wild Variety
1.	Plant height (cm)	91.5±0.47	103.8±0.47	101.2±0.47	110.2±0.47	120±0.47	126.03±0.51	118±0.47
2.	No. of effective tillers (no./m^2)	295±0.47	299±0.47	304±0.47	94±0.47	95±0.47	101±0.47	60±0.47
3.	Panicle length (cm)	23±0.47	22.5±0.47	24±0.47	27±0.47	29±0.47	30±0.47	26±0.47
4.	Dry matter accumulation (g/ plant)	157.7±0.47	158.7±0.47	149.2±0.47	160.1±0.47	161.1±0.47	169.03±0.47	142.9±0.47
5.	Grains per panicle (number/plant)	186.7±0.47	188.7±0.47	183.1±0.47	90.8±0.47	92.4±0.47	98±0.47	43.0±0.47
6.	Grain yield (q/ha)	73.75±0.47	79.4±0.47	71.75±0.47	40.0±0.47	42.3±0.49	44.0±0.47	25.6±0.47
7.	Straw yield (q/ha)	185±0.47	178±0.72	179±0.47	164.8±0.47	162.3±0.36	161.04±0.47	123.3±0.72

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(v/v) orthophosphoric acid 85% and acetonitrile. The linear gradient started at 5% acetonitrile for 2 minutes followed by isocratic elution with 25% acetonitrile over the next 3 minutes. Flow rate was adjusted to 1 ml/ min. Injection volume was 10 µl. Salicylic acid were identified by known standards of calibration curves and also by comparing of the retention times (RT) in the same chromatographic conditions and quantified by the external standard method. The wavelengths for fluorescence detection were chosen in order to give an optimal sensitivity and selectivity to this method.

Plant growth and yield attributes

The crop was harvested in the field when the plants had dried and panicles had matured. The harvested crop was threshed manually. Growth attributing and yield attributing parameters were recorded. Plant growth parameters included plant height, number of tillers/sqm, number of effective tillers, dry matter accumulation. Yield parameters included grain yield, straw yield, panicle length, grains per panicle. Plants were selected randomly to measure height from ground level to the base of the most fully opened leaf in centimeter (cm). Shoots of uprooted plants at harvest stage were sun dried and then oven dried at 60 °C for 2 days to record dry weight of shoot in grams (g). Total number of tillers and effective tillers per plant were recorded at harvest stage and expressed as an average number. Panicle length per plant were recorded at time of harvest and expressed as average number of panicle length per plant. Yield parameters as grain yield, straw yield, grains per panicle were recorded at time of harvest. Total number of grains per panicle were recorded and expressed as average number of grains per panicle. Grain yield was recorded and expressed as quintals per hectare. The total produce was weighed in bundles after harvesting and threshed thereafter. The straw weight was obtained after annulling the weight of the grain from the total bundle weight. Straw yield was expressed as quintals per hectare.

RESULTS AND DISCUSSION

Microfloral profiling of root tissue endophytes of Non-Basmati, Basmati varieties and wild variety

The microfloral profiling of root tissue of Parmal varieties (PR121, PR122 and PR126) and Basmati varieties (Punjab Basmati-3, Punjab Basmati-5, Pusa Basmati 1121) and wild variety (Labra) was performed using various microbiological media as mentioned in 2.1. The results are presented in Fig 1. The pattern of bacterial growth was largely similar in Basmati and Parmal varieties. Varietal differences in cell counts were mostly non-significant. However, behavior of wild variety was markedly different. It had greater abundance of bacteria, bacterial cell counts was always moderately higher than that of Basmati and Parmal varieties. Free living nitrogen fixers were expectedly present in all varieties at all stages of growth of rice. They were more abundant in the wild variety in which they peaked at 60 DAT and later at the time of harvest when their population was significantly higher compared to that in cultivated varieties. The maximum count of free living nitrogen fixers recorded was at 5.3 cfu/g in wild variety compared to the two cultivars- Basmati and Parmal varieties 4.7 cfu/g and 4.66 cfu/g, respectively. Symbiotic nitrogen fixers count was greater in cultivated varieties compared to wild variety at DoT. This difference disappeared at time of harvest. Symbiotic nitrogen fixers peaked at 5.47 cfu/g at time of harvest. Gram negatives were more abundant than Gram positives. Significantly higher population of Gram negatives was recorded at 60 DAT in the wild variety. Later, it balanced

out between all varieties at the time of harvest. Gram positives were comparatively sparse, exhibiting an average cell count of 3.3 cfu/g throughout the growth period of rice. Wild variety had a greater count of spore formers, significantly high at 8.4 cfu/g at DoT compared to 7.1 cfu/g in Basmati and 6.6 cfu/g in Parmal variety. Subsequently, the cell count of spore formers evened out till harvest stage. Total cell count topped cell count of 10.0 cfu/g. Both the cultivated varieties, Basmati and Parmal, recorded comparable cell counts at all stages of growth. Their total viable cell count was greatest at 90 DAT. Wild variety recorded a near static cell count irrespective of growth stage.

Salicylic acid concentration at different stages in cultivation of rice

The comparative presentation of SA concentration at different stages of growth of Parmal, Basmati rice varieties and wild variety is presented in Fig 2. The SA content in root tissue of rice varieties followed a similar pattern in Basmati and Parmal varieties. However, SA content in roots of wild variety was notably different. In Basmati and Parmal varieties, the SA content increased from DoT and peaked at 60 DAT. It was at the lowest (0.04 ug/g in Parmal and 0.08 ug/g in Basmati variety) at 90 DAT. It is pertinent to mention that the rice root endophytic community is fully established by 90 DAT. Subsequently, both varieties exhibited increase in SA content from 90 DAT to the time of harvest. SA content at DoT was below detection level in the wild variety. Afterwards, it increased steadily from 60 DAT to time of harvest, 0.28 ug/g.

Plant growth and yield parameters at harvest stage

All varieties exhibited significant differences with regard to plant growth and yield parameters. These include plant height, number of effective tillers, panicle length, dry matter accumulation, grains per panicle, grain yield and straw yield. The results are presented in Table 1. Average plant height of the basmati and wild variety recorded was comparable, 118.74 cm and 118.0 cm, respectively. It was significantly higher than that of Parmal variety, 98.83. Number of effective tillers, panicle length (cm), dry matter accumulation (g/plant), grains per panicle (number/plant), grain yield (q/ha) and straw yield (q/ha) were all significantly different between cultivated Basmati and Parmal varieties and also between cultivated and wild variety. Effective tillers and grains per panicle impact grain yield. Parmal variety recorded highest number of effective tillers, an average of 299.33/m^2. Consequently, it recorded highest number of grains per panicle, 186.17 per plant and maximum yield of 74.97 q/ha. Wild variety recorded the lowest yield of 25.6 q/ha. Notably, SA content remained consistent in all the growth stages of rice. Apparently, the energy cost for disease resistance is provided by compromising on yield trait.

SA is a plant phenolic compound. It plays a role in signaling pathway that controls local and systemic defense responses. These responses are stimulated by both beneficial and parasitic micro-organisms (Glazebrook, 2005; Van Wees *et al*., 2008). Upon infection or invasion of plant by microbes, Systemic Acquired Resistance (SAR) gets stimulated. SA is an important signaling molecule of SAR (Durrant *et al*., 2004; Van Wees *et al*., 2008). It acts by inducing production of local and systemic pathogen related (PR) proteins which inhibit the growth of the pathogen (Ward *et al.,* 1991). The stimulation of SA is essential during the early stages of plant growth (Herrera-Medina *et al*., 2003; Alonso-Ramirez *et al*., 2014). It protects the plant from microbial invasion and makes it observant against any colonization (Klessig and Malamy, 1994; Ghazijahani *et al*., 2014) by inducing hypersensitivity response (Koornneef *et al*., 2008; Van Wees *et al*., 2008). Absence or inactivation of SA pathway affects the microflora and results in abnormal root microbiome. More importantly, SA signaling is important in recruiting beneficial bacteria from the rhizospheric soil and facilitating colonization of root tissue by them (Lebeis *et al*., 2015). Impact of SA has been reported to effect root colonization by AMF in tobacco plant (Herrera-Medina *et al*., 2003). SA related pathway is suppressed in the face of interaction between plant beneficial fungi (Jacobs *et al.,* 2011) and also in the organization of *Rhizobium*-legume association (Peleg- Grossman *et al*., 2009; Stacey *et al*., 2006).

In the present study, SA content increased from a baseline level at DoT to 60 DAT in the cultivars. It decreased at 90 DAT and peaked at the time of harvest. SA content in the landrace variety was below detection level at DoT. It increased steadily through harvest. Harvest is the time of plant senescence. SA content is commensurate with increase in endophytic bacterial count. SA content decreased at 90 DAT when establishment of root microflora was complete. The decrease in SA concentration for suppression of SA dependent immune response in plants is essential for establishment of symbiotic relation between mycorrhiza and plants for the beneficial association (Lopez-Raez *et al*., 2010; Pozo and Azcon- Aguilar, 2007). The increase in SA content at harvest stage prevents postharvest loss of crops. Comparable SA content recorded in the landrace variety was at all stages which probably is the reason for its greater disease resistance compared to Non-Basmati and Parmal varieties. Both the cultivars exhibited a similar trend of bacterial cell count at all stages of growth. The differences in their cell count were statistically non-significant though. However, cell

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count in root tissue of landrace variety was noticeably different. It revealed greater abundance of bacteria at all stages of growth. It is relevant to mention that tissue culture generated seedlings were used in this study for exacting on putative endophytic bacteria and eliminate bias of all kinds.

Endophytic and rhizospheric microbial community is impacted by both above ground factors as well as below ground factors. These include but are not limited to type of soil, type of crop and its growth stage, soil physical and chemical characteristics, environmental conditions, etc. (Prakamhang *et al.,* 2009). They reported 3.0-6.0 log cfu/gfw of cell (at seedling, vegetative, reproductive stages) count in different plant tissues (leaves, stems and roots). Hongrittipun *et al*. (2014) report 3.47-5.30 log cfu/g of cell count in one-month old seedling of rice. Rice root harbors high population of nitrogen fixers (Mbai *et al*., 2013; Prasanna *et al*., 2011; Mano and Morisaki, 2008). In our study, we recorded 3.6 log cfu/g of nitrogen fixers both free living and symbiotic. Few previous studies have reported higher nitrogen fixer count in soil. Prasanna and co-workers (2011) reported a very significantly higher nitrogen fixer count of 8.0 log cfu/g.

SA directly effects the growth of certain microbes (Liu *et al*., 2019). It modulates root microbiome composition at multiple taxonomic levels from phylum to family (Lebeis *et al*., 2015, Liu *et al*., 2019). Consequently, exogenous application of SA can sculpt bacterial community composition in soil and in endophytic tissue, both qualitatively and quantitatively. It influences microbial community structure of root which occurs by gating of bacteria taxa (Liu *et al*., 2019). Also, it has been reported that endophytic bacterial strains can utilize SA as a growth signal as well as a source of carbon. The results of this study can open new avenues for modulating root microbiome for altering rhizospheric environment which will achieve enhanced crop production and sustainability.

Authors' contribution

Conceptualization and designing of research work (SG); execution of field/lab experiments and data collection (SC); analysis of data and interpretation (SG,SC); preparation of manuscript (SG).

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