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REVIEW ARTICLE

Bioprospecting of pink-pigmented facultative methylotrophic bacteria as a potential bioinoculant for enhancing yield and nutrient uptake in rainfed agroecosystems: A review

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Abstract

Cotton is a valuable fibre and cash crop vital to the Indian economy, both in agriculture and industry. India is one of the world's largest cotton producers and the crop has significant implications for the rural economy and industrial sectors. It provides the basic raw material to cotton textile industry. In India, it provides direct livelihood to 6 million farmers and about 40-50 million people are employed in cotton trading and its processing. Cotton is mainly cultivated as a rainfed crop in Tamil Nadu. Cotton productivity increased for several years before plateauing from 2015. In Tamil Nadu, during 2022-23, cotton was cultivated over 1.72 lakh hectares, with a production of 3.11 lakh bales and a productivity of 313 kg/ha. Currently, cotton cultivation in Tamil Nadu is primarily threatened by low productivity due to severe climate change, biotic stress, rising temperatures and inconsistent rainfall distribution and water availability in arid and semi-arid areas. In dryland agriculture, drought impedes germination, seedling growth, interferes with photosynthesis and increases CO_2 loss through transpiration, thus increasing the competition between vegetative and reproductive aspects for nutrients and carbohydrates. The phyllosphere microflora plays a crucial role in uncovering plant stress mitigation pathways and identifying beneficial microbial strains. However, detailed evidence on the phyllosphere bacterial population of cotton and its role in mitigating abiotic stress remains limited. In this context, the present study focuses on Pink-Pigmented Facultative Methylotrophs (PPFMs), which hold significant potential as sustainable alternatives to conventional chemical inputs for enhancing cotton resilience in rainfed agroecosystems.

Keywords : bioinoculant; cotton yield; nutrient uptake; PPFM; rainfed agro ecosystem

Introduction

The leaf surface area of terrestrial plants, which can potentially be colonized by microbes, is estimated to be around 6.4×10^8 km^2 can support bacterial populations of approximately 10^{25} cells (1). Plants are a potential reservoir of a wide range of structurally and functionally diverse natural compounds, varying from simple esters to more complex molecules such as carbohydrates, polyketides, flavonoids, lignans, terpenoids, alkaloids and tannins (2–5). Bacteria often inhabit diverse environments. The phyllosphere hosts large, complex and dynamic microbial communities, with bacteria being the predominant microbial inhabitants. One such environment is the phyllosphere, where facultative methylotrophic bacteria are commonly found in large numbers (6). PPFMs are Gram-negative, rod-shaped, aerobic bacteria capable of utilizing simple carbon compounds such as formate, formaldehyde and methanol as their sole carbon sources (7, 8). Methylotrophic bacteria utilize single-carbon (C1) compounds for energy and assimilation, playing a crucial role in the global carbon cycle (9). Methylobacteria are found on the roots, leaves and seeds of most land plants and many are believed to be phytosymbionts (10). PPFMs are valuable in agriculture as they enhance crop yield and seed germination, protect plants from pathogens and help crops tolerate drought stress (11). They also play a role in carbon cycling (12), phosphate uptake (13), plant growth regulators (indole acetic acid (IAA) and cytokinins) production (14) and nitrogen fixation in the phyllosphere and rhizosphere of plants (15). For these reasons, they are used as bioinoculants in agriculture (16).

Distinctive features of PPFMs

PPFMs are obligate aerobic, Gram-negative, rod-shaped bacteria that can utilize single-carbon substrates, particularly methanol and methylamine, as well as a variety of multi-carbon compounds for growth. The average size of the bacterium is approximately 1.0 µm in length and 0.5 µm in width. Poly-β-hydroxybutyrate (PHB) granules, the primary storage compound has been detected in the cells of *Methylobacterium* spp. through PHB granule staining. Most studies have indicated that *Methylobacterium* are Gram-negative, although some reports have described them as Gram -indeterminate (17). PPFMs are typically isolated on Ammonium Mineral Salt (AMS) agar medium supplemented with methanol as the sole carbon source.

PPFM-plant symbiosis

The interaction between PPFMs and host plants varies widely, ranging from rhizospheric symbiosis and other associative relationships to leaf-associated and endophytic colonization (18). PPFMs are isolated using the leaf imprinting method on AMS agar medium from a variety of plants, such as neem (19), paddy (20) and cotton (21). Secondly, PPFMs release osmoprotectants, such as sugars and alcohols, onto the surfaces of host plants (22). This matrix could aid in protecting plants from drying out and extreme temperatures. PPFMs can form biofilms and *Methylobacterium* strains can produce quorum-sensing inducers such as N-acyl homoserine lactones. PPFMs are reported to potentially interact with other microorganisms within the host, including phytopathogens. However, only a few studies have demonstrated that the abundance of methylobacteria or PPFMs differs between plant species in these ecosystems. Moreover, previous studies have discussed the presence and role of aerobic methanol-oxidizing bacteria, including PPFMs, in soil ecosystems, highlighting their contribution to carbon cycling (23). Researchers have reported the isolation and characterization of a pink-pigmented, facultative methylotrophic bacterium from rhizosphere soil, demonstrating its potential plant-growth-promoting attributes (24). Scientists have explored the association of methylotrophic bacteria with plants and their potential role in plant growth and stress tolerance (25). Researchers have examined the stoichiometry and energetics of growth in *Methylobacterium* species, providing insights into their metabolic adaptations in rhizospheric environments (26).

PPFMs: bacteria associated with plants

PPFM bacteria establish symbiotic relationships with various plant species and are passed horizontally to the next plant generation via their seeds (27). This relationship benefits plants, as the PPFMs generate cytokinins. Cotton plants that exhibited increased growth also showed higher cytokinin production; however, the bacteria responsible have not been identified (28). It has also been demonstrated that PPFM symbionts produce other growth-promoting factors, including ethylene, auxins and gibberellic acid, which benefit the plants (29). This relationship is a model for plant-microbe interactions. The breakdown of methanol by PPFMs enables plants to thrive in various environments. Without this process, plants would struggle to obtain sufficient carbon for efficient growth. Research also shows that PPFM can degrade other carbon sources and efficiently utilize phosphate, potentially offering further support to plants.

All this evidence has contributed to a better understanding of the distribution of PPFMs in nature, particularly on cotton plants. The beneficial interaction between plants and Methylobacteria can be regarded as an ideal model for symbiotic associations between plants and microbes. Host plants release metabolic by-products, primarily carbon sources in the form of methanol, which are utilized by associated Methylobacteria. In return, these bacteria provide phytohormones that are essential for the growth and metabolism of the host. These mutually beneficial interactions suggest a potential coevolution of the symbiotic bacterial partners. *Methylobacterium* spp. are typically found throughout the plant, particularly on the leaf surfaces, stems, flowers and roots (30). The diversity of *Methylobacterium* in the phyllosphere of *Lolium perenne* was first described in earlier studies. Subsequently, they have been identified as the most dominant phyllosphere population in more than seventy plant species tested and are mostly found as common prokaryotic epiphytes. However, they can colonize plants as endosymbionts (31). Endophytic and intercellular colonization of bacteria facilitate active interactions between bacterial symbionts and the host plant.

Carotenoid pigment production: a key trait of PPFMs in rainfed ecosystems

The production of carotenoid pigments is indeed a noteworthy characteristic of PPFMs in cotton. These pigments are responsible for the pink colouration often observed in these bacteria, which belong to the genus *Methylobacterium*. The carotenoids not only contribute to the bacteria's distinctive appearance but also play important roles in their physiology (32). In the context of cotton plants, PPFMs can influence plant growth and health positively. They are known for their ability to produce plant growth-promoting substances such as cytokinins and for their role in stress tolerance. Their pigment production could be an adaptive advantage, helping them survive and function effectively in the cotton plant environment (33).

PPFMs-mediated plant growth promotion in rainfed ecosystems

PPFMs play a significant role in promoting plant growth through various direct and indirect mechanisms. Numerous *Methylobacterium* species enhance host plant growth by producing IAA and synthesizing auxins and cytokinins, which contribute to plant development. Several studies have documented the role of PPFMs in improving seed germination, seed vigour index, plant yield and systemic resistance (34-36). Additionally, these bacteria exhibit strong biocontrol properties against phytopathogens, protecting plants from harmful diseases and enhancing overall plant vitality. These attributes highlight the potential of PPFMs as plant growth-promoting bacteria for sustainable agriculture (37).

Production of plant hormones by PPFM in rainfed ecosystems

The interaction between plant growth-promoting rhizobacteria (PGPR) and cotton plants plays a vital role in regulating the synthesis and signaling of plant hormones, which are essential for growth and stress adaptation (38). These interactions influence the levels of endogenous phytohormones, enhancing cotton's resistance to pathogens and supporting its overall development. Phytohormones such as salicylic acid (SA) and jasmonic acid (JA) activate defense pathways, inducing systemic acquired resistance (SAR) and producing antimicrobial compounds. Additionally, ethylene (ET) and abscisic acid (ABA) regulate stomatal closure and strengthen cell walls, limiting pathogen entry and spread (39). Soil and plant-associated bacterial groups can synthesize and release one or more phytohormones. Among the different plant growth hormones, auxins are considered the most vital for normal plant growth and development (40). To date, there have been no reports of plant species incapable of synthesizing auxins (41). It is well established that auxins excreted by microorganisms positively influence plant growth (42).

Gibberellic acid (GA), a plant growth hormone, is essential for regulating several growth processes including cell division and tissue differentiation (43), net assimilation rate, dry matter accumulation (44), leaf expansion and elongation, transpiration rate, flowering and photosynthesis (45). GA plays a significant role in regulating plant development and growth, especially under various abiotic stress conditions (46). The plant growth-promoting effects of gibberellins produced by numerous plant growth-promoting bacteria (PGPB) have been documented by various researchers (47). Moreover, the development of PPFM strains engineered to overproduce hormones has the potential to enhance plant growth and development significantly.

The sequestration and transport of Fe^{3-} through siderophores is an effective strategy developed by bacteria to fulfill their iron needs (48). Bacteria produce low molecular weight iron-chelating compounds known as siderophores which facilitate the capture and transport of iron into bacterial cells (49). Siderophore production by rhizospheric microorganism's benefits plants by outcompeting phytopathogens, especially under conditions of limited iron availability (50, 51). These siderophores act as anti-pathogenic factors and can serve as indicators of biocontrol efficiency (52). In a study, the *in vitro* production of siderophores was tested in the pathogen *Xylella fastidiosa* and the PPFM strain *Methylobacterium extorquens*. The findings revealed that the culture supernatants of *X. fastidiosa* lacked both hydroxamate and catechol-type siderophores, while hydroxamate siderophores were present in the supernatants of *M. extorquens*. In citrus plants, *Methylobacterium* spp., which occupy the same ecological niche as *X. fastidiosa* subsp. *pauca*, were found to produce hydroxamate-type siderophores but not catechol-type siderophores (53). Interestingly, the *in vitro* growth of *X. fastidiosa* was enhanced in the presence of siderophores produced by the endophytic *M. mesophilicum*, which shares the same ecological niche. It was also reported the production of siderophores by *M. mesophilicum* strains ARS 1/5 and ARS 1/6 (54). Under laboratory conditions, *Methylobacterium phyllosphaerae* strains MB-5 and CBMB-27 showed positive results to produce amino acid-conjugated hydroxamate-type siderophores. However, neither strain produced catecholate-type siderophores under iron-limited conditions (54, 55).

Nitrogen fixation

Nitrogen is an essential mineral nutrient critical for plant growth and development. It is a fundamental component of various key molecules, including proteins, nucleic acids, chlorophyll and coenzymes. Additionally, nitrogen is integral to ATP, the primary energy carrier in cells (56). Numerous microorganisms, known as diazotrophs, particularly certain eubacteria, contribute significant amounts of nitrogen to the soil through N_2 fixation. These diazotrophic organisms provide fixed nitrogen to plants in exchange for carbon compounds supplied by the plants (57). The positive impact of diazotrophic microorganisms on plant health and productivity has been extensively documented.

Researchers investigated the potential of diazotrophic rice methylotrophs like *Methylobacterium* sp. CBMB20, *Enterobacter* sp. CBMB30 and *Burkholderia* sp. CBMB40 to improve rice seedling growth. These isolates exerted a discernible influence on seed germination, seedling vigour index and biomass production of rice seedlings. *Methylobacterium organophilum*, a thermophilic nitrogen-fixing species isolated from hot spring mud, efficiently fixed di-nitrogen even at elevated temperatures (58). The ability of *Methylobacterium* to fix atmospheric nitrogen and colonize leaf tissues has also been shown to enhance the tolerance of *Jatropha* (a biodiesel crop) under low soil nutrient conditions. The use of nitrogen-fixing *Methylobacterium* has been reported to improve the productivity and green index of *Jatropha* for biofuel production (59, 60).

Phosphorus solubilisation

Phosphorus is a vital yet often limiting nutrient required for biological growth and development (61, 62). It plays a key role in various plant metabolic functions, including photosynthesis, signal transduction, energy transfer (63) macromolecular biosynthesis and respiration (64). Due to its importance, phosphate solubilization is considered as essential as nitrogen fixation in promoting plant growth. Phosphate-solubilizing microorganisms (PSM) aid in converting insoluble phosphate into a plant-available form, which is crucial for sustaining healthy plant function under nutrient-deficient conditions (65). Despite its abundance in soil, phosphorus (P) is largely inaccessible to plants, as it is commonly found in bound inorganic forms (fixed, labile) or organic forms that are also immobilized. However, plants can only absorb phosphorus in its soluble forms, such as mono and dibasic phosphate ions, making their availability critical for proper plant nutrition and growth (66). Phosphate solubilization is a vital process for ensuring phosphorus availability to plants. Since phosphorus in soil is often present in forms that plants cannot access, microorganisms play a key role in converting insoluble inorganic phosphorus fractions into soluble forms that plants can easily absorb (67). This transformation not only improves nutrient availability but also provides a sustainable solution for nutrient supply in agriculture. The use of microorganisms to enhance phosphorus accessibility is gaining recognition as a promising strategy for boosting soil fertility and promoting sustainable agricultural practices (68, 69). PPFMs are known for their multifaceted plant growth-promoting activities, including their potential role in phosphorus solubilization. These bacteria can enhance phosphorus availability by secreting extracellular enzymes such as phytases, nonspecific acid phosphatases and C-P lyases, which break down insoluble organic phosphates into plant-accessible forms. By facilitating phosphorus solubilization, PPFMs contribute to improved nutrient uptake, particularly in phosphorus-deficient soils common in rainfed agroecosystems. Additionally, PPFMs' ability to produce these extracellular enzymes gives them a competitive advantage in the rhizosphere, helping them outcompete harmful pathogens. This dual function, enhancing phosphorus availability and promoting microbial dominance, makes PPFMs a promising bioinoculant for sustainable agriculture. Their integration into cropping systems could improve nutrient-use efficiency, especially in challenging environments with limited phosphorus accessibility (70).

Modulation of ethylene levels in plants

The gaseous hydrocarbon ethylene is a unique phytohormone with several biological roles related to seedling growth, ripening of fruits, germination of seeds, abscission of leaves and petals, organ senescence and biotic and abiotic stress induced responses. Generally, a decrease in levels of ethylene in plants enhances root extension, but increased ethylene levels in plants, especially in fast-growing roots, can hinder important developmental processes, mainly root elongation (71). Thus, the beneficial role of this vaporous hormone is reported at very low concentrations. Elongation of shoot and root is normally inhibited by the action of ethylene. Moreover, stress-regulating activity of ethylene has also been elucidated well (72). Various abiotic stresses such as salinity, drought, water logging and the presence of heavy metals dramatically increase endogenous levels of 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene in plants, which in turn leads to elevated ethylene production (73). The accumulation of excessive ethylene further intensifies stress in plants, resulting in reduced nutrient uptake, impaired water absorption etc. (74 ,75). Only a few research publications on 1-aminocyclopropane-1-carboxylate deaminase (ACCD) activity in *Methylobacterium* spp. exist (76). The inhibiting activity of ACCD on phyllosphere *Methylobacteria* from rice has been detected and assessment of its functional regulatory role in determining ethylene level in rice and tomato seedlings showed that the enzyme activity notably lowers the ethylene level (60–80 %) in the plants (77, 78). Based on the results of a biotic root elongation assay conducted on canola seedlings researchers reported the presence of ACCD activity in *Methylobacterium* spp. (79). Specifically, *M. fujisawaense* exhibited ACCD activity, leading to a significant reduction in ethylene levels in canola seedlings, thereby promoting root elongation. Additionally, *M. oryzae* sp., an aerobic ACCD producing PPFM bacterium, was identified in the stem tissues of rice, highlighting its potential role in plant growth regulation. The isolate was reported to be closely related to *M. fujisawaense*, *M. radiotolerans* and *M. mesophilicum*. *Methylobacterium oryzae* strains CBMB20 and CBMB110 showed significant variation in their ability to metabolize ACC producing 94.5 and 24.7 nmol of α-ketobutyrate mg^{-1} of protein h^{-1} respectively. Seed treatment with these strains increased root length in pepper and tomato plants under gnotobiotic conditions, attributed to their ACC deaminase activity, compared to control plants (80). Additionally, treatment of tomato and red pepper plants with *Methylobacterium* reduced ethylene emission compared to control plants under greenhouse conditions.

PPFM as potential plant-growth promoters in rainfed ecosystems

A plethora of methylotrophic bacterial species are known to live in close association with both terrestrial and aquatic plants, colonizing roots, leaf surfaces, buds and other plant parts. Numerous benevolent attributes of PPFMs have been explored and reported by various researchers. Inoculation of either *Methylobacterium* or methanol spray has shown profound increase in dry matter production and plant height of cotton against uninoculated control (81). Discernable variation in photosynthetic activity was noticed in rice cultivar Co-47 treated with *Methylobacterium* due to increased chlorophyll content, stomatal number and maleic acid content (82). A remarkable improvement in germination was noted compared to uninoculated control when sugarcane true seeds were treated with PPFM strains. Strikingly, the combined application of PPFM through seed treatment, soil drenching and phyllosphere spraying led to increases in plant height, specific leaf area, number of internodes and cane yield (83). ACCD producing *Methylobacterium* was found to reduce the synthesis of ACC, thereby lowering deleterious ethylene levels in canola seedlings grown under gnotobiotic conditions (84). The highest maize cob yield was observed when plants were sprayed with methylotrophic bacteria, highlighting their potential to enhance crop productivity (85, 86).

In another investigation, soybean plants that received both seed inoculation and foliar spray of *Methylobacterium* showed high chlorophyll content (87). In a two-year field experiment, application of PPFM alone was found improving growth attributes like leaf number per plant, chlorophyll content and yield attributes like pod number per plant of snap bean. Moreover, total sugars, ascorbic acid, amino acids and protein content of pods were also increased significantly. Effect of inoculation of *Methylobacterium* spp. possessing ACCD and IAA activity on tomato and red pepper seedling performed under gnotobiotic and greenhouse conditions was found to be comparable to the exogenous applications of synthetic IAA (88). Increased production of IAA by the foliar application of *M. extorquens* MP1 isolated from peach (*Prunus persica* L.) phyllosphere and *M. zatmanii* MS4 from strawberry (*Fragaria ananassa* L.) employing leaf imprint method augmented the growth of tomato plants compared to uninoculated control (89). The combination of multiple plant growth promoting characteristics keeps PPFMs as an attractive microbial tool in agriculture (90, 91). They are categorized as Biosafety Level 1 organisms, as there have been no reports of *Methylobacterium* mediated pathogenicity in plants to date (92). Taking into account their beneficial attributes to host plants, various *Methylobacterium*-based biofertilizers have been launched in the markets. For instance, NewLeaf Symbiotics, a company developing the next generation of agricultural biologicals as biocomplements to existing chemicals, has developed a commercial product composed solely of *Methylobacterium* to accelerate the growth of cotton, tomato, peanut, rice, corn, soybean and wheat (93). Although, many potential *Methylobacterium* strains have been described previously, relatively few products are currently available in the market. Very recently, a seed coating technology using immobilized cells of plant growth promoting *Methylorubrum aminovorans* to improve seed quality of cotton was introduced (94). This novel technology utilizes microbial cells of *M. aminovorans* immobilized in a composite nanofibre matrix composed of chitosan and poly vinyl alcohol (PVA) as an effective localized delivery system. A similar study introduced a seed invigouration technique for groundnut plants using electrospun PVA nanofibre containing immobilized microbial cells of *M. aminovorans* (95). The application of encapsulated *M. aminovorans* successfully enhanced root colonization and subsequently improved seed germination, seedling vigour and growth of groundnut plants.

PPFMs as biological control agents of plant diseases

PPFMs have demonstrated biocontrol potential against soil-borne phytopathogens, alongside their growth-promoting effects on plants (96). Their role in triggering induced systemic resistance (ISR) against a variety of plant pathogens is also well documented (97, 98). Seed treatment or foliar spray of *Methylobacterium* on rice induced the expression of pathogenesis-related proteins, which protected the plants against sheath blight pathogen *Rhizoctonia solani* under pot culture conditions (99). PPFMs bring about several physiological changes in plants, making them more resistant to pathogens. *M. extorquens* CO-47 induced the accumulation of peroxidase, polyphenol oxidase, phenylalanine lyase and phenols in plants and subsequently suppressed the pathogen *R. solani*. *Methylobacterium* spp. treated groundnut plants challenged with *Aspergillus niger* or *Sclerotium rolfsii* resulted in enhancement of seed germination and seedling vigour index. It also caused the increase in the activities of β-1,3- glucanase, phenylalanine ammonia lyase (PAL) and peroxidase (PO). Also, presence of five isozymes of polyphenol oxidase and PO were noticed in *Methylobacterium* treated plants when challenged with the pathogens (100). Application of *Methylobacterium* strains on tomato induced the defence response against the plant pathogen *Ralstonia solanacearum* (101). As already stated, *Methylobacterium* spp. synthesize anti-phytopathogen factors, such as siderophores (102). The antagonistic effect observed against the tested fungal pathogens may be partly due to the production of salicylic acid, a type of siderophore, produced by PPFM isolates. This has been demonstrated in *M. oryzae* CBMB20, which, when co-inoculated with *Pseudomonas syringae* pv. tomato in tomato plants, showed enhanced defense responses compared to control or *M. oryzae*-only treatments under both growth chamber and greenhouse conditions (103). The volatile antibiotics produced by *Methylobacterium* ceases mycelial growth of *S. rolfsii*, *Fusarium udum*, *F. oxysporum*, *Pythium aphanidermatum*, *Colletotrichum capsici* and *Cercospora capsici* and inhibit the growth of *Xanthomonas campestris* with various biocontrol efficacies under *in vitro* conditions. *Methylobacteria* isolate CO-47 hindered the mycelial growth of *R. solani* and the inhibition zone measured under *in vitro* conditions was 1.4 cm (104). Methylotrophs inhabiting mangrove sediment have been found to be powerful biocontrol agent against root rot pathogen *Macrophomina phaseolina*. The inoculation of PPFM isolates to chilli grown under field conditions remarkably reduced the anthracnose disease caused by *Colletotrichum capsica* (105).

Another interesting finding made was the biocontrol potential of *M. fujisawaense* against *Meloidogyne incognita* (Kofoid and White) chitwood race 3. *M. fujisawaense* filtrate was found to be highly effective in inhibiting egg hatching and reducing root penetration of *M. incognita* in tomato plants (106, 107). Published literature on biocontrol activity of *Methylobacterium* has so far been consistent and conclusive. The ISR observed in plants treated with methylotrophic bacteria supports the potential use of PPFM strains as biological control agents against plant diseases.

Conclusion

Pink-Pigmented Facultative Methylotrophs (PPFMs) hold significant potential as bioinoculants to improve nutrient uptake and cotton yield in rainfed agro ecosystems. PPFMs have special qualities that can greatly improve cotton production, especially in regions that are prone to drought. Their diverse functions in fostering plant resilience and growth make them good candidates for sustainable agricultural practices.

Future perspectives

Development of drought-resilient bioformulations

Advancing PPFM-based bioinoculants tailored for drought-prone regions can enhance nutrient uptake and crop productivity under water-limited conditions.

Integration with sustainable agricultural practices

Combining PPFMs with organic amendments and conservation agriculture can promote eco-friendly and resilient cropping systems.

Field trials and large-scale adoption

Extensive field evaluations and farmer participatory research are needed to validate the efficacy of PPFMs and promote their widespread use in rainfed farming.

Genomic and biotechnological advancements

Exploring the genetic and metabolic pathways of PPFMs can facilitate the development of bioengineered strains with enhanced plant-growth-promoting traits suited to diverse agroecosystems.

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Authors' contributions

SB contributed to writing the original draft of the manuscript. SS provided corrections and supported the manuscript. AK, PA, SD, KS, MV, TR, JJ, PK, SM, MS and RJP advised on data processing and interpretation of the results. Each author reviewed the manuscript and participated in the data analysis. All authors have read and agreed to the published version of the manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no competing interests related to this study.

Ethical issues: None

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