



# ***Piriformospora indica*: A Helper Endophytic Fungus in Enhancing Growth and Nutrient Status in Crops**

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## **Authors' contributions**

*This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.*

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## **ABSTRACT**

Many microorganisms including root endophytes establish symbiotic relationships with their host plants and play a crucial role in maintaining better soil health and plant growth. Most of the crops are responsive to manures and fertilizers; however, the indiscriminate use of inputs especially chemical fertilizers can result in adverse environmental impacts which may degrade soil health and quality, affect rhizosphere micro-environment and cause nutrient imbalances. These adverse effects can be reduced by adopting new microbial-based technological practices, especially the use of biofertilizers, which are renewable and ecofriendly alternatives to chemical fertilizers that promote plant growth by enhancing the availability of plant nutrients. *Piriformospora indica*, a helper mycorrhiza like endophytic fungus has received immense importance over the preceding decades because of its ability to efficiently promote plant growth through enhanced nutrient uptake, bioactive substance accumulation, crop protection from pest and disease attack. Additionally, *P. indica* also

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helps to improve plant resistance to biotic stresses such as bacterial, fungal, viral and nematode diseases and abiotic stresses like drought, salinity and heavy metal toxicity. Apart from the fungal biomass, derivatives of *P. indica* such as cell wall extract as well as culture filtrate also acts as an excellent source for plant growth promotion. Here, we explore the mechanisms involved in *P. indica* mediated growth promotion as well as biotic and abiotic stress mitigation which includes enhanced nutrient acquisition and its translocation, increased efficiency of photosynthesis and modulation of phytohormones involved in growth and development. With the increasing demands for safer agricultural products and foods without the use of chemical fertilizers and pesticides, this paper also identifies research needs for making suitable biocontrol or biofertilizer formulations by utilizing the functional abilities of *P. indica*.

**Keywords:** Endophyte; *Piriformospora indica*; growth promotion; stress mitigation; nutrient acquisition; crop protection.

## 1. INTRODUCTION

Endophytes are micro-organisms that reside inside the living host tissues for at least a part of their life cycle without causing any apparent symptoms in the plant (Wilson, 1995). They are either beneficial or commensal in nature and can be isolated after surface disinfection from the host plant, and they cause no harmful effects on the growth of plants (Hallmann et al., 1997). The term "endophyte" was originated from the Greek words "end on" (within) and "python" (plant) and was first used by Anton de Bary in 1866. They mostly demonstrate mutualism by supplying or facilitating nutrient uptake and shielding the plants from many biotic and abiotic challenges, while in return they receive protection and nourishment from their host plants (Kumar and Dara, 2021). Both fungal and bacterial endophytes exist in nature. The fungal endophytes include *Piriformospora indica*, Arbuscular mycorrhizal fungi (*Glomus* spp., *Funneliformis mosseae*), *Sebacina vermifera*, *Beauveria bassiana*, *Mortierella hyalina* and the bacterial endophytes include *Bacillus* sp., *Pseudomonas* sp., *Rhizobium* sp., *Azospirillum amazonense*, *Serratia liquefaciens*, *Methylobacterium extorquens*, *Enterobacter aerogenes* (Hallmann et al., 1997).

Among them, *Piriformospora indica*, a helper mycorrhiza like root colonizing beneficial endophytic Agaricomycetes fungus belonging to order Sebaciales (Basidiomycota), was obtained from the rhizosphere of *Zizyphus nummularia* and *Prosopis juliflora*, woody shrubs in the Thar Desert in Northwest India (Verma et al., 1998; Varma et al., 1999). A wide spectrum of crop species, including various agronomical, horticultural, medicinal and ornamental plants are known to be colonized by *P. indica* (Das et al.,

2012; Qiang et al., 2012; Ye et al., 2014; Anith et al., 2018). Numerous studies have demonstrated that *P. indica* could promote the growth of various crop plants, stimulate the uptake of nutrients, and increase plant stress tolerance, thereby offering a very promising opportunity for application in sustainable agricultural practices (Anith et al., 2011; Unnikumar et al., 2013; Varkey et al., 2018; Athira and Anith, 2020; Paul et al., 2021). Additionally, *P. indica* has also been reported to improve crop tolerance to a number of biotic stresses like pest and disease attack as well as abiotic stresses including drought, salinity, low temperature and heavy metal toxicity (Waller et al., 2005., Baltruschat et al., 2008; Sun et al., 2010., Varma et al., 2012) (Table 1).

## 2. ROOT COLONIZATION BY *Piriformospora indica*

*Piriformospora indica* root colonization can be divided into four stages. The process of fungal root colonization begins with the germination of chlamydospores and extracellular growth. Later, hyphae penetrate epidermal or cortical cells and establish an early biotrophic colonization phase, which are preceded by intercellular colonization. The complete intactness of cell organelles and invagination of the plasma membrane marks the early and late biotrophic stages. Subsequently during cell death-associated colonization phase, the biotrophically colonized cells die. Host cell death is indicated by organelle disruption, while the plasma membrane still surrounds intracellular hyphae. Intracellular sporulation takes place in epidermal and cortical cells at about 14 days after inoculation. However, the fungus never invades the vascular tissues and at cellular level, this fungus colonizes living root cells by its direct penetration (Jacobs et al., 2011).

**Table 1. *Piriformospora indica* mediated growth promotion as well as biotic and abiotic stress mitigation in different plants**

Host plant	Growth promotion	Biotic stress tolerance	Abiotic stress tolerance	Reference
<i>Oryza sativa</i> (Rice)	Enhancement in shoot length, root length as well as dry weight of plants	Reduction in bacterial blight disease incidence	Increased tolerance to salinity	Jogawat et al., 2013; Kundu et al., 2022
<i>Triticum aestivum</i> (Wheat)	Increased uptake of nitrogen and phosphorus	Protection against powdery mildew caused by <i>Blumeria graminis</i> f.sp. <i>tritici</i> and Eye spot disease caused by <i>Pseudocercospora herpotrichoides</i>	Increased tolerance to cadmium stress, reduces zinc deficiency stress	Serfling et al., 2007; Baltruschat et al., 2008; Shahabivand et al., 2012; Abadi and Sepehri, 2015
<i>Zea mays</i> (Maize)	Increase in biomass production and induce phyto-promotional effects	Reduction in the root disease caused by <i>Fusarium verticillioides</i>	Improvement in salinity and drought tolerance	Stein et al., 2008; Kumar et al., 2009; Zhang et al., 2018
<i>Hordeum vulgare</i> (Barley)	Enhancement in seed viability, grain yields and vegetative growth	Protection against root rot diseases caused by <i>Fusarium culmorum</i> , <i>Cochliobolus sativus</i> and <i>Rhizoctonia solani</i>	Salinity, drought and low temperature stress tolerances	Waller et al., 2005; Serfling et al., 2007; Qiang et al., 2012; Harrach et al., 2013; Ghabooli et al., 2014; Murphy et al., 2014
<i>Nicotiana tabacum</i> (Tobacco)	Enhanced biomass production, increased uptake of nitrogen, phosphorus and zinc	Reduction in the incidence of herbivorous insects attack	Increased tolerance to cadmium stress	Hui et al., 2014; Abdelaziz et al., 2019
<i>Lycopersicon esculentum</i> (Tomato)	Increase in seedling growth and fruit biomass	Protection against fusarium wilt caused by <i>Fusarium oxysporum</i> , black root rot by <i>Thielaviopsis basicola</i> , verticillium wilt by <i>Verticillium dahlia</i> and yellow leaf mosaic by Pepino mosaic virus	Tolerance to osmotic stress and chloride toxicity	Qiang et al., 2012; Fakhro et al., 2010; Al-Absi and Al-Ameiri, 2015
<i>Brassica rapa</i> (Chinese cabbage)	Promotes root and shoot growth as well as lateral root formation	Reduction in the incidence of black spot disease	Drought tolerance	Sun et al., 2010

Host plant	Growth promotion	Biotic stress tolerance	Abiotic stress tolerance	Reference
<i>Brassica napus</i> (Rapeseed)	Increased uptake of nitrogen, phosphorus, sulphur, zinc and manganese, increase in plant biomass, oil yield and quality, earliness in bolting and flowering	Decrease in the root rot disease incidence	Tolerance to drought and water logging stress	Chen et al., 2013; Zheng-zhu et al., 2017
<i>Arabidopsis thaliana</i>	Enhanced seedling development and seed production	Protection against powdery mildew caused by <i>Golovinomyces orontii</i> , root rot by <i>Rhizoctonia solani</i> , verticillium wilt by <i>Verticillium longisporum</i> , leaf blight by <i>Alternaria brassicae</i>	Drought tolerance	Shahollari et al., 2007; Sherameti et al., 2008; Stein et al., 2008; Knecht et al., 2010; Johnson et al., 2013
<i>Piper nigrum</i> (Black pepper)	Earliness in flowering and spike setting, increase in total oleoresin and piperine content in berries	Reduction in foliar infection caused by <i>Phytophthora capsici</i>	-	Anith et al., 2018; Paul et al., 2021
<i>Manihot esculenta</i> (Cassava)	Increase in plant growth and tuber yield	Reduction in root rot disease caused by <i>Lasiodiplodia theobromae</i> and <i>Fusarium</i> sp., reduction in cassava mosaic disease severity and viral load caused by cassava mosaic virus	-	Subhash et al., 2025
<i>Colocasia esculenta</i> (Taro)	Increase in growth parameters such as plant height, number of leaves, leaf length and leaf breadth	Protection against taro leaf blight caused by <i>Phytophthora colocasiae</i>	-	Lakshmipriya et al., 2016

*Piriformospora indica* and plant roots recognition is mediated by signal responses. A series of host responses to symbiotic fungi are based on an efficient immune system within the plants (Boller et al., 2009). Intracellular colonization of *P. indica* stimulates mode-triggered immunity (PTI), which could be modulated by phytohormones, such as ethylene, salicylic acid (SA) and jasmonic acid (JA) (Khatabi et al., 2012). The combination of both ethylene and JA promotes the colonization of *P. indica*, whereas their combination blocks SA accumulation (Khatabi et al., 2012).

The colonization process of *P. indica* was seriously destroyed by the inactivation of some components in the ethylene pathway (Camehl et al., 2013). The weak ethylene signals promote hyphal growth while, salicylic acid thioglycoside inhibits the growth of mycelia (Varma et al., 2001). During the interaction with roots, *P. indica* was found not stable in mutant plants with ascorbic acid reductase, hence it's very important to maintain low ascorbic acid levels in roots (Vadassery et al., 2009). After the fungal colonization, gibberellin, auxin and other hormones levels in plants was found increased in varying degrees (Schafer et al., 2009; Camehl et al., 2013). The increase in  $Ca^{2+}$  concentration was found to be an early signal of root colonization by the fungus (Vadassery et al., 2010).

During the lethal stage of *P. indica* colonization, the transduction of endoplasmic reticulum stress signals was inhibited by the spores that eventually led to a caspase-dependent cell death mediated by vacuoles which implies that endoplasmic reticulum dysfunction in roots triggered by *P. indica* is a strategy to kill plant cells (Qiang et al., 2012). *P. indica* colonization appears mainly in the near root elongation zones and rarely at the top of the roots (Kumari et al., 2003). The maturity degree of roots cells and the colonization pattern of the fungus are closely associated with each other (Boller et al., 2009; Unnikumar et al., 2013).

### 3. PLANT GROWTH PROMOTION BY *Piriformospora indica*

*Piriformospora indica* mediated stimulation of plant growth is by the means of extensive absorption and mobilization of nutrients from soil to the aerial plant parts (Shahollari et al., 2007). The main important characteristic feature of any mutualistic plant-microbe interactions is the

capability of the microbial endosymbionts to assimilate nitrogen (N), phosphorus (P) and micronutrients that limit plant growth and to share these nutrients with the plant in return for a carbon source derived from photosynthesis (Varma et al., 2012). Root colonization by *P. indica* resulted in an increase in the plant growth, early flowering, higher seed yield and secondary metabolites production in different crop species (Varma et al., 2012). Significant improvement in the growth and yield of several medicinal plant species such as *Aloe vera*, *Artemisia annua*, *Bacopa monnieri* and *Linum album* was also found on inoculation with *P. indica* (Rai et al., 2001; Prasad et al., 2013; Kilam et al., 2016). *P. indica*-induced seed germination and development has been reported in several crop plants like barley, tomato and Arabidopsis (Varma et al., 2012).

The major processes involved in *P. indica* mediated plant growth promotion is through the enhanced nutrient uptake and translocation, greater photosynthetic efficiency, modification of growth and development of related plant hormones (Oelmuller et al., 2009). Increased contents of chemical compounds and secondary metabolites were reported in *P. indica*-colonized *Coleus forskohlii* (Das et al., 2012). Improvement in growth and yield as well as piperine and oleoresin content in the berries of black pepper was also reported on inoculation with *P. indica* (Anith et al., 2018).

*Piriformospora indica* leads to the enhancement in nutrient uptake, especially nitrogen and phosphorous in many plants (Yadav et al., 2010; Kumar et al., 2011). Isolation, identification and functional characterization of a high affinity phosphate transporter (PiPT) from *P. indica* revealed its essentiality for phosphate transport to the host plant (Yadav et al., 2010). Knockdown (KD) transformants were reported to transport a significantly lower amount of phosphate to the host plant than wild-type *P. indica*. Higher phosphate contents were found in plants colonized with wild-type *P. indica* than that of non-colonized and plants colonized with KD-PiPT *P. indica* (Varma et al., 2012). In *Anthurium andraeanum*, plants colonized with *P. indica* was found to absorb more P and exhibit greater photosynthetic efficiency when compared to the uncolonized plants (Hui-Feng et al., 2019).

*Piriformospora indica*, as a potent phosphate mobilizer, generates phosphatase enzymes that breaks down the phosphate ester linkages of

organic phosphates and insoluble polyphosphates (Malla et al., 2004). The process of P-solubilization in soil involves both acid and alkaline phosphatases. Alkaline phosphatases are only found in the hyphal membrane of the fungal symbiont and are involved in P assimilation, whereas acid phosphatases are found in both symbionts localized in plasma and cell membranes of mycorrhizal roots, and involved in P uptake (Fries et al., 1998). Acid phosphatases produced by *P. indica* were reported to mobilize and assist in phosphate-acquisition, and growth promotion in *Lycopersicon esculentum* (Sarma et al., 2011).

Sherameti et al. (2005) reported that the co-cultivation of *Nicotiana tabacum* and Arabidopsis seedlings with *P. indica* was accompanied by a huge transfer of N from the agar plates into the aerial part of the seedlings. This effect is associated with activation of the NADH-dependent nitrate reductase (NR), the key enzyme which plays an important role in nitrate acquisition in plants. *P. indica* colonization also causes early protein changes in the endoplasmic reticulum and the plasma membrane as well as increased expression of the enzymes  $\beta$ -glucosidase (PYK10),  $\beta$ -glucuronidase gene (uidA), and nitrate reductase (Nia2), as well as the starch-degrading enzyme glucan-water dikinase (SEX) in roots, which is involved in early starch degradation events in *N. tabacum* and Arabidopsis plants (Varma et al., 2012).

Efficiency of photosynthesis is improved by increased content of carotenoid, chlorophyll a, photosynthetic electron transport, enhanced level of photochemical and non-photochemical quenching in *P. indica* colonized plants. Recent findings indicate that *P. indica* improves the level of phytohormones which promotes plant growth, differentiation, and immunity (Johnson et al., 2014).

The colonization of *P. indica* influences the production of plant hormones such as auxin, cytokinin, ethylene, gibberellin and abscisic acid which plays a crucial role in enhancing the plant growth and development (Adarsh et al., 2024). *P. indica* colonization induces IAA production and affects the accumulation of JA which helps to improve the meristem ability of longan root (Cheng et al., 2022). In many plant species such as barley, Arabidopsis and Chinese cabbage, this fungus modulates various gene expressions associated with auxin and cytokinin (Xu et al., 2018). Modulation of phytohormone levels by *P.*

*indica* also helps to enhance plant's defense mechanisms against a wide range of pathogens and thereby enhancing plant growth.

#### 4. BIOTIC STRESS MITIGATION BY *Piriformospora indica*

Recently, *P. indica* has been found to provide extensive bio-protection to economically important agricultural and horticultural crops against variety of pests and disease attack (Varma et al., 2012). Plant stress tolerance can be conferred via *P. indica*-mediated activation of antioxidant defense components and altered expression of genes linked to stress (Gill et al., 2016). Furthermore, by controlling defense gene expression and sRNA production, *P. indica* can use signal transduction and RNA interference to create both local and systemic plant resistance to fungal and viral pathogens (Li et al., 2023).

The biotic stress protection by *P. indica* was initially reported in barley. The *P. indica* colonized barley plants were observed to be resistant against *Blumeria graminis* and *Fusarium culmorum* infection (Waller et al., 2005). Additionally, the antagonistic activities of *P. indica* were reported to directly inhibit root pathogens in many plants (Franken et al., 2012). Plants treated with *P. indica* exhibited significant defense against the root-pathogenic fungus *Cochliobolus sativus* (Oelmüller et al., 2009). When confronted with the virulent root and seed pathogen *Gaeumannomyces graminis*, *P. indica* demonstrated significant disease control mechanism (Serfling et al., 2007). Although the chemical nature of this inhibitory component was unknown at the time, *P. indica* totally inhibited the growth of pathogenic fungi, suggesting that the fungus may be a potential agent for biocontrol of root infections.

Recently *P. indica* was reported to combat cassava root rot disease, a complex disease caused by the combination of several pathogens including *Lasiodiplodia theobromae*, *Fusarium* sp. and *Cunninghamella elegans*. An increase in growth and yield parameters with a decrease in the disease incidence was observed in *P. indica* inoculated plants when challenged with root rot pathogens (Subhash et al., 2025).

Systemic resistance against the biotrophic leaf pathogen *Blumeria graminis* f.sp. *hordei* was induced by *P. indica* colonized *Hordium vulgare* roots (Molitor et al., 2011). Pathogen damage to the host was also significantly reduced in *P.*

*indica*-colonized tobacco plants, which demonstrated a notable decrease in disease spots against *Alternaria longipes*, *Colletotrichum gloeosporioides*, *Pythium ultimum*, *Rhizoctonia solani*, *Phytophthora parasitica*, and *Ralstonia solanacearum* (Hui et al., 2014). *P. indica* also showed its biocontrol potential against leaf blight disease caused by *Phytophthora colocasiae* in Sree Kiran and Muktakeshi varieties of taro by reducing the disease incidence (Lakshmipriya et al., 2016).

The upregulation of specific genes such as leucine-rich repeat receptor kinases (LRR-RKs) and WRKY transcription factors (WRKY-TFs) confer strong resistance to powdery mildew infection due to *P. indica* colonization in barley seedlings (Molitor et al., 2011). The pathogenesis-related (PR) genes expression was induced due to *P. indica* colonization in rice offering disease resistance to the blast disease caused by *Magnaporthe oryzae* (Li et al., 2023). In wheat plants, inoculation with *P. indica* induced systemic resistance against *Fusarium graminearum* or *Rhizoctonia cerealis* by increasing H<sub>2</sub>O<sub>2</sub> content, antioxidase activity, relative water content, and membrane stability index compared to the plants only inoculated with *F. graminearum* or *R. cerealis* and control. In addition to this, the differentially expressed genes related to disease resistance, such as WRKY and MAPK, were also upregulated as a result of *P. indica* colonization (Li et al., 2022).

Recently, *P. indica* was found to efficiently suppress cassava mosaic virus disease. Plants treated with *P. indica* showed significant reduction in the cassava mosaic disease severity and viral load compared to the control plants marking the first report of cassava mosaic disease management using this beneficial fungal endophyte (Subhash et al., 2025). According to Fakhro et al. (2010), *P. indica* protects crop plants from fungal and viral diseases, promoting improved growth and development. Following adjustments to inoculation methods, such as inoculum density and plant stage, it was demonstrated that *P. indica* reduces tomato shoot Pepino mosaic virus concentration.

Apart from mediating the suppression of various fungal diseases, *P. indica* also helps to manage certain bacterial and nematode infections. The involvement of *P. indica* was reported in the suppression of a bacterial wilt pathogen *Ralstonia solanacearum* in tomato plants (Athira and Anith, 2020). Antagonism of cyst nematode

infection and development in *Arabidopsis thaliana* by *P. indica* has been reported (Daneshkhah et al., 2013). It was also observed that inoculation with this endophytic fungus reduced egg density of soybean cyst nematode (Bajaj et al., 2016).

## 5. ABIOTIC STRESS MITIGATION BY *Piriformospora indica*

*Piriformospora indica* has been extensively reported to improve crop tolerance to a number of abiotic stresses including drought, salinity, low temperature and heavy metal toxicity (Baltruschat et al., 2008; Sun et al., 2010). *P. indica* colonization also leads to the activation of abiotic stress responsive genes (DREB2A, CBL1, RD29A) and osmo-protectants such as proline, glycine betaine (Gill et al., 2016).

**Drought tolerance:** The faster upregulation of drought tolerance related phospholipase D $\delta$ , CBL1 and HAT in addition to the enhanced activities of ROS scavenging enzymes localized in cell membranes, chloroplasts, peroxisomes and mitochondria were observed in the *P. indica*-colonized seedlings (Sherameti et al., 2008). Similarly, when drought stress was mimicked in *P. indica* colonized Chinese cabbage plants by exposing them to 20% polyethylene glycol (PEG), the colonized-plants could very well survive as a result of the increased peroxidases, catalases and superoxide dismutase activities in the leaves, whereas the non-colonized plants could not survive (Sun et al., 2010). The expression levels of the drought-related genes DREB2A, CBL1, ANAC072 and RD29A were also upregulated in the drought stressed leaves of *P. indica* colonized plants (Sun et al., 2010).

**Salinity tolerance:** Root colonization by *P. indica* also helps to tolerate salinity stress in many plants. Zarea et al. (2012) reported that the fungus could tolerate higher salt concentration of 200-400 mM under *in vitro* condition. Under salt stress condition, *P. indica* maintains a high antioxidative environment to detoxify ROS. In this process, the activities of different superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase, peroxidase, monodehydroascorbate reductase and dehydroascorbate reductase were induced in *P. indica*-colonized plants (Baltruschat et al., 2008; Zarea et al., 2012). The increased salt tolerance in *P. indica* colonized rice plants were due to higher content of the photosynthetic pigments Chl a, Chl b and carotenoids in addition to the

enhanced levels of osmolytes such as proline and polyamines (Jogawat et al., 2013). *P. indica*-colonized barley, wheat, rice and tobacco plants were able to survive in moderate salt (NaCl) concentration of 100 mM to 300 mM with higher biomass production whereas this concentration was detrimental to the uncolonized control plants (Waller et al., 2005; Baltruschat et al., 2008).

**Heavy metal tolerance:** The environmental pollution due to heavy metals poses a serious threat to plant growth and development. The mutualistic association between *P. indica* and its host plants helps to remediate heavy metal-contaminated soils. *P. indica* plays an important role in uptaking heavy metals from the rhizospheric region and accumulating them on the root surface whereas, it does not mediate the translocation of heavy metals to the above ground plant tissues (Li et al., 2023). The *Arabidopsis* and wheat plants colonized by *P. indica* were found to perform better under cadmium stress conditions (Shahabivand et al., 2012). Biopriming with *P. indica* ameliorates cadmium stress in rice by lowering oxidative stress and cell death in root cells (Dabral et al., 2019). In *Cassia angustifolia*, *P. indica* helps to tolerate copper stress and also helps to protect *Panicum miliaceum* plants from copper-induced oxidative damage (Nanda and Agrawal 2018; Saman and Sepehri., 2022).

**Low temperature tolerance:** *Piriformospora indica*, which is commonly associated with plants growing under extreme hot conditions of Thar desert of western Rajasthan, India also interacted with plants at high altitudes. Experiments which were conducted at the Defense Institute of Higher Altitude Research (DIHAR), DRDO, Leh Ladakh, India at an altitude of 3,300m showed an increased seed germination of vegetables such as cabbage, endive, radish, beet root, onion and Swiss chard even up to 100 per cent in a period of 25 days at extreme low temperature (-30 to 4°C) on inoculation with *P. indica*, whereas not a single seed germinated in the untreated control (Murugan, 2011).

## 6. DERIVATIVES OF *Piriformospora indica*

The derivatives of *P. indica* includes cell wall extract (CWE) as well as culture filtrate obtained from *P. indica*. The cell wall extract from *P. indica* promotes tuberization in potato (*Solanum tuberosum* L.) via enhanced expression of Ca<sup>2+</sup> signaling pathway and Lipoxigenase Gene

(Upadhaya et al., 2013). The 4% *P. indica* CWE application produced more Valerenic acid (VA), a sesquiterpene constituent responsible for medicinal properties derived from valerian (*Valeriana officinalis*) when compared to 2% CWE treated plants at the exposure time of 72 h (Ghesmati et al., 2017). The CWE from the fungus was also found to promote growth and induce intracellular calcium elevation in roots of wild-type seedlings of *Arabidopsis thaliana* but not of seedlings from *P. indica*-insensitive mutants (Vadassery et al., 2009).

Apart from the fungal biomass, culture filtrate also acts as an excellent source for plant growth promotion. Not only the mycelium in association with roots but also the culture filtrate of the mycelium contains fungal exudates, minerals, hormones, enzymes and proteins (Verma et al., 1998). *In vitro* experiments have shown that even very small amounts (50 mL/20 mL) of culture filtrate are sufficient to promote root and shoot growth. The culture filtrate was also found effective in enhancement of seed germination, growth of the seedlings and also in inhibiting the growth of a few virulent root fungal pathogens tested (Varma et al., 2012).

The culture filtrate of *P. indica* promoted overall growth and seed production of *Helianthus annuus* Sun gold and *H. annuus* Japanese gold varieties in greenhouse and the treatment also increased the oil content of seeds by 50% to 70% in these two varieties of *H. annuus* plants (Bagde et al., 2011). The podophyllotoxin and 6-methoxypodophyllotoxin (the lignans) concentrations were maximally improved by 3.8 times (233.8 mg/L) and 4.4 times (131.9 mg/L) in comparison to control cultures, respectively, upon addition of 3.0% (v/v) filter-sterilized culture filtrate of *P. indica* to the hairy root cultures of *Linum album* for exposure time of 48 h (Kumar et al., 2012). The highest vegetative growth (e.g. plant height, root length, number of leaves per plant, root and shoot dry weights) and physiological traits (e.g. relative water content, proline, anthocyanin content, chlorophyll a, and chlorophyll b) were observed with 7.5 mL of *P. indica* culture filtrate in both aeroponic and soil culture media than the control Chicory (*Cichorium intybus* L.) plants (Rashnoo et al., 2020).

## 7. INTERACTION WITH RHIZOSPHERIC AND OTHER BENEFICIAL MICROBES

Multiple microbial interactions involving bacteria and fungi in the rhizosphere have shown to

provide enhanced biocontrol in comparison with single biocontrol agents (Whipps, 2001). *P. indica* interacts with a diverse group of microorganisms such as *Sebacina vermifera*, *Pseudomonas fluorescens* (rhizobacteria), *Chlamydomonas reinhardtii*, and other soil fungi (*Aspergillus niger*, *A. sydowii* and *Rhizopus stolonifer*) (Gill et al., 2016). Sharma et al. (2008) demonstrated that association of *P. indica* with *Rhizobium radiobacter* promotes the growth of barley seedlings and developed systemic resistance to the powdery mildew fungus *Blumeria graminis*. Co-inoculation of a phosphate solubilizing bacterium *Pseudomonas striata* and *P. indica* showed a synergistic effect on chickpea (Meena et al., 2014). A consortium of rhizobacteria and *P. indica* was also found to suppress the root-knot nematode parasite in tomato (Varkey et al., 2018). The mycoparasite *Trichoderma harzianum* inhibits *P. indica* root colonization and growth *in vitro*, but inoculation of pepper plants with *P. indica* and subsequently with *T. harzianum* resulted in higher plant dry weights compared to single inoculations (Anith et al., 2011). *P. indica* either alone or in combination with *S. vermifera*, *Trichoderma viride* and *T. harzianum* was found to be very effective in reducing the Fusarium wilt disease severity of lentil (Dolatabadi et al., 2012).

## 8. CHALLENGES AND FUTURE PROSPECTS

Despite of the several functional benefits of *Piriformospora indica*, the development of suitable bioformulations with improved shelf life and with easy and effective delivery of this fungus to the host plants still remains as a challenge. The beneficial microorganisms applied as biofertilizers or as biocontrol agents play an important role in today's agriculture by improving soil fertility and crop productivity. Hence, the future line of research should focus on the production of suitable bioinoculant formulations using *P. indica* with increased shelf life. Furthermore, the signal mechanisms and pathways related to the increased antioxidant defense systems, interaction between *P. indica* and other microorganisms as well as identification of novel pathogenicity or stress responsive genes needs to be investigated.

## 9. CONCLUSION

*Piriformospora indica* is a multifunctional root endophytic fungus widely used as a model organism to understand the mechanisms and evolution of mutualistic symbiosis. The fungus

colonizes a wide range of hosts and provide multifaceted facilities to the plants, such as nutrient uptake, disease resistance, stress tolerance and growth promotion involving value addition. It also enhances the ability of plants to tolerate various biotic and abiotic stresses such as drought, salinity, heavy metal, extreme temperature and pathogens attack. Root colonization by *P. indica* was found to provide better nutrient-acquisition abilities as well as improvement in plant growth and productivity as a result of enhanced root proliferation due to indole-3-acetic acid production, thereby providing better plant performance in all aspects. Additionally, through signal transduction, *P. indica* can induce both local as well as systemic resistance to fungal and viral plant diseases. With the development of suitable bioformulations, all these functional properties of *P. indica* can be utilized for better plant growth and soil health. Hence, the future line of research should focus on the development of such formulations which also paves the way for promoting environmentally friendly and economically viable sustainable agricultural practices.

## DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

## COMPETING INTERESTS

Authors have declared that no competing interests exist.

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