Review Article

Harnessing the beneficial fungus *Piriformosporaindica*for climate resilient crop production: A Review

Abstract

Piriformospora indica, classified as an Agaricomycetes fungus, has garnered significant interest due to its remarkable capacity to enhance plant growth, fortification, and resilience to stress factors. Its ability to inhabit various plant species stems from its direct influence on plant hormone signalling pathways. This colonisation stimulates increased root proliferation by generating indole-3-acetic acid, facilitating better nutrient absorption and ultimately leading to heightened crop yields. Furthermore, *P. indica* initiates resistance against fungal and viral threats while reinforcing the plant's antioxidant defences, fortifying its resilience to stressors. It aids in successfully acclimating micro-propagated plants upon transplantation. It can establish complex symbiotic relationships, including tripartite symbiosis, which enhances the population dynamics of plant growth-promoting rhizobacteria. Overall, *P. indica*is a multifaceted facilitator of plant growth, a source of biofertilisation, a barrier against pests and diseases, a regulator of biological functions, and a promoter of overall plant development. Understanding the physiological and molecular mechanisms underlying the mutualistic interaction between *P. indica* and crop plants can provide valuable insights for enhancing crop protection and productivity, thereby contributing to the sustainability of agricultural practices.

Keywords:*Piriformospora indica;* nutrient use efficiency; biotic stress; abiotic stress; resistance

Introduction

Various microorganisms within natural ecosystems engage in interactions with plants to acquire nutrients, spanning from neutral to either harmful or beneficial, as documented by Chandra and Enespa (2019) and Mitter*et al*. (2013). Most plants within these ecosystems exhibit a robust symbiotic relationship with mycorrhizal fungi and fungal endophytes, as highlighted by Mack and Rudgers (2008). These fungi demonstrate diverse lifestyles, including biotrophy, necrotrophy, and hemi-biotrophy, as Schäfer *et al*. (2009) outlined. One such fungus, *Piriformospora indica*, originating from the rhizosphere soils of desert woody shrubs in Rajasthan, India, is a versatile organism that is easily cultivable andcolonises plant roots as an endophyte, as elucidated by Rajput *et al*. (2022) and Varma *et al*. (2012). As a root endosymbiont belonging to Sebacinales, *P. indica* functions as a biotrophic mutualist, conferring various benefits to plants, including nutrient uptake, disease resistance, stress tolerance, and growth promotion, as reported by Johnson *et al*. (2014) and Gill *et al*. (2016). Furthermore, *P. indica* has been attributed with multifaceted roles, such as facilitating biological hardening during transplantation and enhancing the synthesis of valuable compounds in plants, as Nouh *et al*. (2020) observed. Its ability to be easily cultured in bioreactors makes it a suitable candidate for producing effective biofertilisers, as Pi*et al*. (2015) noted. The potential of *P. indica* inoculum for commercial applications in crop enhancement is promising, offering opportunities to reduce reliance on chemical fertilisers and bolster resistance to various stresses, as Khalid *et al*. (2017) suggested.

Recent research has underscored the role of *P. indica* in enhancing biomass, seed germination, plant growth, and crop productivity, thereby positioning it as a valuable tool for agricultural improvement (Wani *et al*., 2015). This fungus contributes to plant welfare by facilitating nutrient absorption and adaptation to harsh environmental conditions such as drought, high temperatures, and soil salinity (Nouh *et al*., 2020). This article underscores the fungus's significant biological and molecular traits and explores its potential applications in biotechnology as a plant growth-promoting mycorrhizal fungus (PGPF). The paper provides an overview of *P. indica*'s mechanisms for colonising roots, its symbiotic relationship with plants, involvement in programmed cell death, genetic makeup, and biotechnological relevance. It also assesses *P. indica*'s interactions with other microorganisms and its regulatory functions in plant metabolism, stress response, and defense mechanisms while identifying areas in current research that warrant further investigation.

Root Colonisation

The expansive range of *P. indica*, encompassing vascular plants and mosses, suggests deploying highly efficient colonisation strategies (Qiang *et al*., 2012). Insights into its lifestyle and mechanisms for root colonisation have been gleaned from interactions with diverse plants such as Hordeum vulgare and Arabidopsis thaliana (Unnikumar*et al*., 2013). Colonisation proceeds with dense extracellular hyphae enveloping roots without penetrating vascular tissues or directly invading living root cells (Novero *et al*., 2008). Microscopic examination reveals no discernible impairment in colonised roots.Distinct interaction types occur across various root regions, with older zones exhibiting a higher prevalence of intracellular hyphae (Smith *et al*., 2001). The activity of host cells is pivotal for effective nutrient exchange. This colonisation pattern contrasts with arbuscular mycorrhizal fungi, which predominantly colonise younger root sections (Nongbri*et al*., 2012).

The initial comprehensive genomic examination unveiled a mutualistic symbiont, *P. indica*, exhibiting a dual-phase lifestyle as it colonises both living and deceased roots of Hordeum vulgare (Akum, 2015). Utilising microarray analysis, researchers elucidated a two-step root colonisation strategy of *P. indica*, characterised by precisely regulated expression of gene sets associated with its lifestyle (Zuccaro *et al*., 2011). notably, around 10% of fungal genes induced during biotrophic colonisation encoded putative small secreted proteins (SSP), including lectin-like proteins and members of a *P. indica*-specific gene family (DELD) harbouring a conserved seven-amino acid motif at the C-terminus (Lahrmann & Zuccaro, 2012). DELDs were associated with transposable elements in gene-sparse, repeat-abundant genome regions, resembling effectors observed in other filamentous organisms (Varma *et al*., 2013).

These revelations contribute to a deeper comprehension of the development of biotrophic plant symbionts, suggesting gradual transitions from saprotrophy to biotrophy in the evolutionary trajectory of mycorrhizal associations originating from decomposer fungi. *P. indica*'sbiotrophiccolonisation pattern encompasses a broad suppression of root innate immunity, facilitating its successful establishment (Desisa, 2017). Molecular and genetic analyses have demonstrated that roots, like leaves, possess a robust innate immune system, with the suppression of immunity by *P. indica* being imperative for colonisation success (Jacobs *et al*., 2011). Investigations involving H. vulgare and Arabidopsis mutants deficient in gibberellic acid (GA) and jasmonic acid (JA) metabolism, respectively, have indicated an enhanced root immune response and diminished colonisation (De Bruyne *et al*., 2014).

P. indica predominantly relies on JA-mediated suppression of early immune responses and other defence pathways, such as salicylic acid (SA) and glucosinolate-related pathways (Xu and Oelmüller, 2018). Mutants impaired in SA and glucosinolate defences exhibit increased susceptibility to *P. indica*. The disruption of endoplasmic reticulum (ER) integrity by *P. indica* potentially interferes with the secretion of immunity-associated proteins, suppressing immune signalling and facilitating colonisation (Qiang *et al.*, 2012). With the genome of *P. indica* now available, the possibility of identifying effector molecules targeting immune signalling components exists.

Plant Interaction and Calcium Ions

Mutualistic and commensal relationships in fungi exhibit parallels during their initial infection and colonisation phases (Lastovetsky*et al.*, 2020). Understanding the mechanisms of recognition and early signalling is imperative for plants to discern between beneficial and detrimental microbes that impact plant physiological processes. Upon recognising these symbionts, there is a rapid surge in intracellular calcium levels, marking an early signalling event. Calcium ions function as secondary messengers in diverse plant signalling pathways, influencing plant responses (Aldon *et al.*, 2018). Mutants unable to respond to *P. indica* exhibit compromised calcium elevation, affecting growth promotion (Vadassery and Oelmüller, 2009). Autoclaved cell wall extract from *P. indica* induces calcium elevation and fosters growth in various plant species (Jogawat*et al.*, 2020). The significance of root colonisation is underscored by autoclaved cell wall extract's induced calcium elevation in roots (Johnson *et al.*, 2019). Furthermore, the extract elicits specific plant responses, such as tuberization in potatoes, through the upregulation of calcium-dependent proteins and lipoxygenase mRNA expression (Cheng *et al.*, 2018).

At the interface between plants, *P. indica* engages in signal exchange that modulates phosphorus influx and calcium efflux within plant cells (Lee *et al.*, 2011). These signals originating from endophytes can initiate programmed cell death or stimulate growth and development via phytohormones (Pérez-Alonso *et al.*, 2020). Plants with mutations impairing gibberellic acid (GA) and jasmonic acid (JA) metabolism exhibit decreased colonisation and inhibited growth (Pinski *et al.*, 2019). During programmed cell death (PCD), calcium and phytohormones regulate gene expression, with *P. indica*colonisation resulting in DNA fragmentation and cell shrinkage (Prasad *et al.*, 2022). Structural alterations in Arabidopsis roots during cell death associated with *P. indica*colonisation may stem from the induction of endoplasmic reticulum (ER) stress and suppression of the unfolded protein response (UPR) (Simoni *et al.*, 2022).

Genome Level

Comparing the genome of *P. indica* with that of other fungi reveals the presence of both biotrophic and saprotrophic characteristics (Zuccaro *et al.*, 2011). During the colonisation of Arabidopsis roots, *P. indica* undergoes a biotrophic phase followed by cell death, ultimately not leading to any disease symptoms. *P. indica*utilises these deceased cells for intracellular sporulation (Zhang, 2014). Analysis of colonisedH. vulgare roots has unveiled distinctive gene regulation during various stages of colonisation, with numerous genes induced by symbiosis being specific to *P. indica* (Zhang *et al.*, 2018). Plant hormones such as jasmonic acid (JA) and ethylene are released from root prime shoots to enhance disease resistance (Bhatt *et al.*, 2020). In combating powdery mildew fungus, up-regulation of JA and ethylene signalling pathways, rather than salicylic acid (SA) signalling, is observed (Pimentel *et al*., 2021).

Programmed Cell Death

In general, plant-programmed cell death (PCD) represents a natural reaction to various physiological challenges triggered by internal or external stimuli (Williams and Dickman, 2008). It constitutes a metabolically regulated mechanism pivotal for plant development. Plant PCD resembles animal apoptosis, encompassing chromatin condensation, cell shrinkage, and DNA fragmentation (Ebeed and El-Helely, 2021). The colonisation of roots by fungi entails both a biotrophic growth phase and a phase-dependent on cell death (Qiang *et al*., 2012). Previous investigations into *P. indica*colonisation in plant roots indicates a comparable pattern of biotrophic and cell death-dependent phases, potentially employed by the fungus for intracellular sporulation (Gill *et al*., 2016).In contrast to pathogen-induced HR, cell death was observed during *P. indica*colonisation might not signify a robust plant defence response, as suggested by the feeble and transient upregulation of defence marker genes (Eichmann *et al*., 2010). Furthermore, hallmark indicators of HR, such as accumulation of reactive oxygen species (ROS) and whole-cell autofluorescence, are lacking in roots colonised by *P. indica* (Jacobs *et al*., 2011).

Transmission electron microscopy has revealed that cells remain viable during fungal penetration, undergoing structural modifications as colonisation progresses (Mansfield *et al*., 2019). This implies that fungal colonisation entails more than merely targeting diseased cells. Although host cells ultimately perish upon colonisation, the strategy does not solely rely on the presence of dead cells. Evidence indicates that the colonisation process is contingent upon host cell demise, as demonstrated by the diminished colonisation of roots in plants overexpressing the negative cell death regulator BI-1 (Dickman *et al*., 2013). The upregulation of BI-1 in plants infested with fungi correlates with fungal proliferation, underscoring BI-1's involvement in plant defence and cell viability. BI-1, which participates in integrating endoplasmic reticulum (ER) stress, sustains cell integrity and viability under adverse conditions (Almanza *et al*., 2019).Moreover, the ER plays a crucial role in processing immunity-related proteins, including the pattern recognition receptor (Xu *et al*., 2012). *P. indica* induces ER stress in roots, inhibiting the unfolded protein response pathway (UPR) while initiating a pro-apoptotic signalling cascade due to the incapacity of colonised cells to alleviate ER stress (Qiang, 2010). Vacuolar collapse is essential for *P. indica*-induced cell death and root colonisation, facilitated by vacuolar processing enzymes (VPEs) (Qiang *et al*., 2012). Arabidopsis mutants lacking VPEs exhibit decreased fungal colonisation, emphasising the significance of vacuolar collapse in cell death and colonisation (Hatsugai*et al*., 2015). *P. indica* employs a two-phase colonisation strategy involving biotrophic adaptation and ER stress-induced caspase-dependent vacuolar cell death for successful symbiosis with Arabidopsis (Gill *et al*., 2016).

The broad host range of *P. indica* may stem from its interactions based on general recognition and signalling processes (Waller *et al*., 2008). Screening of Arabidopsis mutants unresponsive to its growth promotion and enhanced seed production was conducted to pinpoint plant genes affected by the fungus (Salas-Marina *et al*., 2011). It was observed that the presence of *P. indica* did not impact the growth and seed production of a T-DNA insertion line in PYK10 despite increased root colonisation compared to wild-type roots (Sherameti*et al*., 2008). The expression of LRR1 is elevated in wild-type roots when in the presence of *P. indica*, whereas plant defensin1.2 (PDF1.2) expression remains unaffected.

Conversely, PDF1.2 expression rises with diminished PYK10 levels, while LRR1 expression does not (Mandyam and Jumpponen, 2013). PYK10 constrains root colonisation by *P. indica*, suppressing defence responses and fostering conditions conducive to mutual interaction between the two symbiotic partners (Trillas and Segarra, 2009).

Seed Germination, Growth and Development

Piriformospora indica has substantially improved growth and yield across various crops, horticultural specimens, and medicinal plants (Johnson *et al*., 2014). Its presence promotes seed germination, development, and productivity while enhancing viability even in unfavourable environments (Khalid *et al*., 2019). Additionally, it facilitates early germination in vascular plants and influences seed-oil yield in Helianthus annuus (Tarte *et al*., 2022). Colonisation of plant roots by *P. indica* has been associated with increased seed yield in various plant species (Su *et al*., 2017). In medicinal plants, its presence is deemed essential for enhancing the production of chemical compounds and secondary metabolites (Zhao *et al*., 2022). *P. indica* has been found to boost the production of anticancer drugs and overall biomass productivity in diverse plant species (Ansari *et al*., 2013).Furthermore, *P. indica*-mediated enhancements have been observed in the growth and biomass of various crop plants (Khalid *et al*., 2019). Its ability to produce auxin stimulates root growth and influences gene expression differentially across different plant species (Xu and Oelmüller, 2018). Additionally, it stimulates the synthesis of secondary metabolites, such as pentacyclic triterpenoids, in suspension cultures of certain plants (Nouri *et al*., 2023). Overall, *P. indica* demonstrates potential as a biopriming agent for augmenting plant biomass growth (Mensah *et al*., 2020).Researchers at Kerala Agricultural University conducted experiments utilising a growth medium containing *P. indica* fungus mixed with various components to improve nutrient utilisation efficiency in rice cultivation. The most effective blend, consisting of paddy soil, farmyard manure (FYM), and coir pith compost in equal proportions, significantly enhanced rice seedling growth compared to standard conditions (Adarsh *et al*., 2023a,b).

Plant Growth Promotion

The interaction between *P. indica* and various crops mirrors that of arbuscular mycorrhizal (AM) fungi, resulting in growth promotion manifested through amplified root and shoot biomass, augmented root hair proliferation, and enhanced vegetative growth, flowering, and seed yield (Ansari *et al*., 2013). This symbiotic association mutually benefits both partners by modulating gene expression, protein synthesis, and metabolite production. *P. indica* facilitates nutrient absorption, fortifies resistance against environmental stresses, and stimulates plant growth. A myriad of crops, spanning from maize, wheat, rice, and barley to sugarcane, along with the model and medicinal plants, demonstrate favourable responses to *P. indica* inoculation, characterised by increased biomass, root proliferation, and yield (Johnson *et al*., 2014). These advantageous effects are reproducible under diverse growth conditions, underscoring the potential of *P. indica* for augmenting commercial crop production. Beyond greenhouse and field settings, *P. indica* exhibits beneficial impacts on tissue culture-raised plantlets, augmenting shoot and root biomass, survival rates, and the content of bioactive compounds such as Artemisinin in Artemisia annua (Baishya *et al*., 2015).

Mechanisms in Growth Promotion

Research on the interaction between *P. indica* and diverse model plants and mutants has revealed that the fungus stimulates growth through enhancements in nutrient uptake and translocation, improvements in photosynthesis efficiency, and modulation of phytohormones associated with growth and development (Xu and Oelmüller, 2018). Nutrient uptake and translocation represent pivotal facets of symbiotic interactions between plants and microbes, wherein microbial endosymbionts assimilate vital elements like nitrogen, phosphorus, and micronutrients necessary for plant growth, exchanging them for carbon derived from photosynthesis (Kaur and Kaur, 2018). *P. indica* fosters growth by effectively transporting, absorbing, and mobilising nutrients from the soil, encompassing nitrogen, phosphorus, potassium, sulfur, magnesium, iron, zinc, manganese, and copper (Paul *et al*., 2023). Notably, it exhibits particular proficiency in mobilising phosphate, a critical mineral nutrient for plants, through the production of enzymes such as phosphatases, which degrade insoluble polyphosphates and organic phosphates, thereby rendering phosphorus more accessible to plants (Dipta *et al*., 2019). The fungus demonstrates adeptness in utilising various phosphate sources, underscoring its role as both a mobiliser and a solubiliser of phosphorus in soil (Adhya *et al*., 2015).

P. indica improves plant growth in Arabidopsis by facilitating the absorption of phosphorus (P) from the soil (Aslam *et al*., 2019). The PiPT gene, essential for phosphate transportation, is identified in plants colonised by *P. indica* (Ngwene*et al*., 2016). Furthermore, *P. indica* triggers the expression of phosphate transporters in Arabidopsis and mung bean plants, resulting in elevated levels of nitrogen (N), phosphorus (P), and potassium (K) (Sehar *et al*., 2023). The interaction between the fungus and the roots induces changes in protein composition, enhancing the expression of enzymes involved in nutrient assimilation (Franken, 2012). Additionally, nitrogen uptake and assimilation are enhanced by *P. indica*colonisation, with increased nitrate reductase activity observed in Arabidopsis and tobacco roots (Li *et al*., 2023). In contrast to arbuscular mycorrhizal fungi (AMF), *P. indica* promotes nitrate uptake rather than ammonium (Fu *et al*., 2021). *P. indica* also facilitates the mobilisation of micronutrients from the soil, thus supporting plant growth and development (Aslam *et al*., 2019).

Increased Photosynthetic Efficiency

Various chlorophyll (Chl) content and fluorescence parameters indicate plant health and photosynthetic activity (Pavlovic *et al*., 2015). Plants inoculated with *P. indica* exhibited elevated levels of Chl a and carotenoids (Ghorbani *et al*., 2018). Furthermore, in Arabidopsis, colonisation by *P. indica* resulted in increased electron flow in PSII and heightened levels of both photochemical and non-photochemical quenching (Li *et al*., 2021).

ModulatingPhytohormone Levels

Plant hormones such as auxin, cytokinin, ethylene, abscisic acid, and gibberellins are indispensable in regulating plant growth and organ development (Sezgin and Kahya, 2018). These hormones significantly influence growth in plant species like Arabidopsis, barley, and Chinese cabbage when influenced by the presence of *P. indica* (*P. indica*) (Xu and Oelmüller, 2018). Promoting growth in Chinese cabbage and barley correlates with heightened levels of auxin and gibberellins in the roots colonised by the fungus (Lee *et al*., 2011). However, the levels of auxin in leaves remain unaffected. Furthermore, cytokinins, particularly trans-zeatin, are pivotal in promoting growth induced by *P. indica* in Arabidopsis (Vadassery*et al*., 2008). The fungus modulates various gene expressions associated with auxin and cytokinin in diverse plant species. Apart from phytohormones, other factors secreted by *P. indica* also contribute to growth promotion in Arabidopsis, Chinese cabbage, and tobacco (Hua *et al*., 2017). The intricate interplay of diverse phytohormones and their signalling networks is pivotal for establishing compatible endosymbioses between *P. indica* and plants (Pérez-Alonso *et al*., 2020).

Nutrient Acquisition

The soil harbours a diverse array of microorganisms, including algae, bacteria, and fungi, which actively participate in chemical processes essential for the growth and survival of plants, such as the carbon and nitrogen cycles, nutrient uptake, and soil development (Abinandan*et al*., 2019). Plants significantly influence the microbial communities in the soil, particularly in the rhizosphere, through carbon input via root exudates (Huang *et al*., 2014). Due to their immobility, plants encounter challenges such as nutrient scarcity, salinity, drought, and pathogen attacks, leading them to form associations with beneficial microorganisms to alleviate these stressors (Enebe and Babalola, 2018). Symbiosis with beneficial fungi assists in nutrient acquisition by plant roots, enhancing soil fertility and crop yield (Phillips, 2017). Similarly, endophytic fungi like *P. indica*, akin to mycorrhizal endosymbionts, have been recognised as growth enhancers for various plant species (Varma *et al*., 2012).The beneficial impacts of endophytic colonization with P indica were apparent in the modified root structure, showcasing increased root volume, length, and depth in summer rice (Mani *et al*., 2023b).

Phosphorus Acquisition

Phosphorus (P), an essential mineral nutrient, constitutes approximately 0.5% of the dry weight of plant cells and serves various functions in regulation, structure, and energy transfer (Malhotra *et al*., 2018). Plants encounter difficulties accessing soil P primarily due to its predominantly insoluble form, which impedes crop production globally (Balemi and Negisho, 2012). They acquire P through direct uptake and associations with mycorrhizal fungi (Smith *et al*., 2015). Colonization by *P. indica.* boosted the absorption of phosphorus from the soil into the plant, leading to the growth of an extensive root system characterized by increased volume (Mani *et al*., 2023a).*P.indica*facilitates the uptake and transfer of P to the host plant through an energy-dependent process, which involves the production of acid phosphatases aiding in the access of insoluble P reserves (Johri *et al*., 2015). While high-affinity phosphate transporters have been identified in various plant and fungal species, the lack of stable transformation systems in arbuscular mycorrhizal (AM) fungal species poses a challenge to understanding (Ferrol *et al*., 2019). The functionalcharacterisation of a phosphate transporter in *P. indica* underscores its significance in transporting P to the host plant. However, the transfer mechanism remains ambiguous, hypothesised to occur at the interface between the plant and fungus, necessitating the involvement of two transporters (Verma *et al*., 2022).

Accounts of *P. indica*'s participation in phosphate transfer and its role in enhancing host plant growth exhibit discrepancies. *P. indica* enhances phosphate uptake and promotes Arabidopsis growth akin to mycorrhizal fungi (Aslam *et al*., 2019). The involvement of *P. indica* in phosphate transfer to Zea mays was evidenced, suggesting a molecular mechanism involving PiPT (Yadav*et al*., 2010). However, despite an increase in grain yield independent of phosphorus and nitrogen levels, no discernible improvement in phosphate supply was noted in the *P. indica*-Hordeum vulgare symbiosis (Achatz *et al*., 2010). Phosphate levels significantly influenced Z. mays biomass when colonised by *P. indica* (Rane *et al*., 2015). Moreover, *P. indica*'s growth promotion was more pronounced under low phosphate conditions, indicating its potential for enhancing crop productivity in phosphate-deficient soils (Wu *et al*., 2019).RT-PCR analysis suggested the involvement of PiPT in phosphate transport, contingent upon its availability (Yadav *et al*., 2010). The phosphate transfer mechanism from *P. indica* to plants remains partially understood, with hypotheses proposing cytoplasmic streaming or bulk flow through external hyphae (Varma *et al*., 2012).

The previously discussed outcomes may originate from the host-specific behaviour of *P. indica*, as investigations have been conducted across various crop plants. A more extensive array of host plants is required to determine whether *P. indica* and PiPT demonstrate host specificity (Qiang *et al*., 2012). Using*P. indica* and PiPTcan bolster crop enhancement efforts and serve as a model for investigating molecular mechanisms and plant phosphate uptake (Gill *et al*., 2016). The authors propose that P. India's strategy for root colonisation involves programmed cell death, suggesting that phosphate released into deceased cells could be assimilated by neighbouring living cells and distributed throughout the plant (Johnston-Monje and Raizada, 2011).

Gene Regulatorand Mineral Uptake

The fungus facilitates nitrate/nitrogen absorption in plants and modulates source-sink relationships by increasing the expression of specific genes. Plants hosting *P. indica* exhibit elevated rates of CO2 assimilation, consequently promoting additional sinks in a balanced manner (Franken, 2012). Moreover, *P. indica*colonisation has been linked to increased N, P, and K levels in chickpeas and black lentils while mitigating Fe and Cu deficiencies in sugarcane (Liu *et al*., 2020). The presence of the receptor kinase in Arabidopsis roots undergoes modification upon colonisation, leading to enhanced uptake of labelled phosphorus (Shi *et al*., 2022). This mutualistic interaction fosters plant growth and development by influencing diverse regulatory and structural processes and facilitating energy transfer. Additionally, a reduction in phosphate content was observed in maize plants colonised by a *P. indica* mutant lacking a phosphate transporter (Yadav *et al*., 2010).

Abiotic and Biotic Stress Tolerance

Extensive research has been conducted on *P. indica* due to its ability to bolster crop resilience against various abiotic stresses, including salinity, low temperature, and heavy metal toxicity (Ansari *et al*., 2013). The adverse effects of moisture stress could be substantially reduced through the advantageous relationship between rice and the root endophyte P. indica in rice (Mani *et al*., 2023b).It has been documented to enhance tolerance to high salinity in Triticum aestivum and drought stress in Arabidopsis seedlings, Chinese cabbage, and strawberries (Gill *et al*., 2016). The presence of *P. indica* has been associated with the activation of defence-related genes, genes responsive to abiotic stress, and osmoprotectants (Khalid *et al*., 2019). Moreover, *P. indica* has evolved mechanisms to deliver effectors intracellularly to facilitate microbial infection and influence host metabolism (Rafiq*et al*., 2013). These effectors are pivotal in initiating and perpetuating symbiosis, enabling the fungus to manipulate the plant's defence mechanism (Selin *et al*., 2016). Specific proteins such as PIIN_08944 have been identified among these effectors, aiding plant colonisation by suppressing the salicylate-mediated basal resistance response (Sharma *et al*., 2018). Expression of PIIN_08944 in Arabidopsis thaliana and Hordeum vulgare has been shown to dampen the activation of immune pathways elicited by flg22, impacting pattern-triggered immunity (PTI) and the salicylic acid (SA) defence pathway (Akum *et al*., 2015). PIIN_08944 facilitates root colonisation by *P. indica* by interfering with the host plant's basal immune responses (Singh *et al*., 2021). Additionally, *P. indica* has been observed to modulate antioxidant defence enzymes and other components of the ROS-scavenging system, thereby enhancing plant tolerance to various stresses and providing protection against pathogens (Nath *et al*., 2016;Varkey etal., 2018; Athira and Anith, 2020).

*Piriformospora indica*is pivotal in safeguarding plants against diverse biotic stresses, such as fungi, bacteria, and viruses (Ansari *et al*., 2013). Upon encountering pathogens, this fungus triggers the upregulation of defence-related genes in host plants, including pathogenesis-related genes and those involved in jasmonate and ethylene signalling (Panda *et al*., 2019). It protects barley plants from root damage inflicted by Fusariumculmorumand shoots infection by Blumeriagraminis (Waller *et al*., 2007). Furthermore, the colonisation of roots by *P. indica* induces systemic resistance against leaf pathogens across various plant species, as evidenced by the elevation of defence-related gene expression (Pedrotti *et al*., 2013). The fungus *P. indica* demonstrates promise in bolstering plant resistance against fungal diseases (Ansari *et al*., 2013). In H. vulgare plants colonised by *P. indica*, resistance to fungal pathogens like F. culmorumand Cochliobolussativus is observed (Johnson *et al*., 2014). Plants treated with *P. indica* also defend against Fusariumculmorumand Blumeriagraminis (Khalid *et al*., 2019). Colonisation by *P. indica* elicits systemic resistance in H. vulgare against biotrophic leaf pathogens (Waller *et al*., 2008). Additionally, *P. indica* has proven effective in biocontrol against T. aestivum and lentil diseases caused by various pathogens (Rabiey, 2016). Greenhouse experiments involving T. aestivum have shown reducedleaf, stem, and root disease incidence upon colonisation with *P. indica* (Lin *et al*., 2019). Moreover, *P. indica* enhances resistance to powdery mildew in Arabidopsis through JA signalling and positively modulates plant defence responses (Vahabi*et al*., 2013).The establishment of *P. indica* within plant hosts triggers the activation of the antioxidant system, thereby bolstering crop resilience against diverse stressors (Aslam *et al*., 2019). *P. indica* exhibits bio-protection against numerous pathogens in wheat and maize and the synthesis of secondary metabolites as natural pesticides (Jha and Yadav, 2021). The interaction between A. thaliana roots and *P. indica* prompts ethylene production, influencing the stability of advantageous traits (Liu *et al*., 2020). Ethylene also facilitates *P. indica*'scolonisation of plant roots through signalling mechanisms, underscoring the significance of ethylene signalling in establishing symbiosis between the fungus and the host plant (Camehl*et al*., 2010).

Reactive Oxygen Species Modulation

Piriformospora indica has been demonstrated to enhance stress tolerance in various crops, including barley, wheat, maize, tomato, and lentil, by augmenting phosphate uptake through elevated levels of alkaline phosphatase and acid phosphatase enzymes in the rhizosphere (Aslam *et al*., 2019). Research indicates that *P. indica* enhances stress tolerance in wheat, barley, and maize by regulating reactive oxygen species (ROS) generation and antioxidant defence pathways (Nath *et al*., 2016). ROS generation and defence-related responses are initially activated during the early stages of mycorrhizal associations but diminish after establishing the symbiotic relationship (Song *et al*., 2011). Hydrogen peroxide (H2O2) triggers defence responses, yet its production is suppressed in *P. indica*-colonized roots under favourable conditions, promoting growth responses (Sood *et al*., 2021). Initially, exudates from *P. indica* induce ROS generation and accumulation of stress-responsive hormones, but upon physical contact, defence responses decrease, and stomata reopen (Vahabi*et al*., 2015).

This interplay between ROS generation, scavenging, signalling, and mycorrhizal association ultimately enhances plant resilience under stress conditions.

Conclusion

Piriformospora indica, akin to a whispered muse in the realm of fungi, demonstrates remarkable adaptability as it weaves its tendrils through a tapestry of plant species, deftly manipulating the symphony of hormonal signals to fortify their defences against fungal and viral maladies. Within its enigmatic embrace, it assumes multifaceted roles: an adept gleaner of nutrients, a sentinel against diseases, a bulwark against stresses, and a maestro orchestrating the crescendo of growth. Its presence within the sanctum of medicinal flora kindles the alchemy of secondary metabolites, casting a spell of both commerce and biotechnological wonder.In the grand tableau of fungal kin, *P. indica* stands as a polymath, embodying traits of both the symbiotic and the saprophytic. Across a verdant expanse of botanical companions, its colonisation stratagems unfurl like delicate petals, nurturing growth and bestowing bounty upon crops and flora alike. As a steward of balance, it assumes the mantle of bio-control, an arbiter of stress responses, and a custodian of the genetic lexicon governing metabolism, mineral uptake, resistance, and fortification.In the microcosm of nano(bio)technological inquiry, revelations bloom like delicate blossoms, offering glimpses into the intimate dances shared between plant and fungus. As the horizon of inquiry beckons, the future's clarion call resounds: to plumb the depths of root symbiosis, to decipher the enigmatic language of effector-like proteins, to unveil the secrets of symbiosis and pathogenicity genes anew, thus unlocking the boundless potential of *P. indica* in shepherding crop plants through the tempests of stress.

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