

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

Abstract

Piriformosporaindica, 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 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: *Piriformosporaindica*; 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 [10]. Most plants within these ecosystems exhibit a robust symbiotic relationship with mycorrhizal fungi and fungal endophytes. These fungi demonstrate diverse lifestyles, including biotrophy, necrotrophy, and hemi-biotrophy. One such fungus, *Piriformosporaindica*, originating from the rhizosphere soils of desert woody shrubs in Rajasthan, India, is a versatile organism that is easily cultivable and colonises plant roots as an endophyte, as elucidated by [42]. As a root endosymbiont belonging to Sebaciales, *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 [17].

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 [34] observed. Its ability to be easily cultured in bioreactors makes it a suitable candidate for producing effective biofertilizers. 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. Studies have 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. This fungus contributes to plant welfare by facilitating nutrient absorption and adaptation to harsh environmental conditions such as drought, high temperatures, and soil salinity [34].

Root Colonisation

51 The expansive range of *P. indica*, encompassing vascular plants and mosses, suggests
52 deploying highly efficient colonisation strategies. Insights into its lifestyle and mechanisms
53 for root colonisation have been gleaned from interactions with diverse plants such as
54 *Hordeum vulgare* and *Arabidopsis thaliana*. The activity of host cells is pivotal for effective
55 nutrient exchange. This colonisation pattern contrasts with arbuscular mycorrhizal fungi,
56 which predominantly colonise younger root sections.

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58 The initial comprehensive genomic examination unveiled a mutualistic symbiont,
59 *P. indica*, exhibiting a dual-phase lifestyle as it colonises both living and deceased roots of
60 *Hordeum vulgare*. Utilising microarray analysis, researchers elucidated a two-step root
61 colonisation strategy of *P. indica*, characterised by precisely regulated expression of gene sets
62 associated with its lifestyle. Around 10% of fungal genes induced during
63 biotrophic colonisation encoded putative small secreted proteins (SSP), including lectin-like
64 proteins and members of a *P. indica*-specific gene family (DELD) harbouring a conserved
65 seven-amino acid motif at the C-terminus. DELDs were associated with transposable
66 elements in gene-sparse, repeat-abundant genome regions, resembling effectors observed in
67 other filamentous organisms [55].

68
69 These revelations contribute to a deeper comprehension of the development of
70 biotrophic plant symbionts, suggesting gradual transitions from saprotrophy to biotrophy in
71 the evolutionary trajectory of mycorrhizal associations originating from decomposer fungi.
72 Biotrophic colonisation pattern of *P. indica* encompasses a broad suppression of root innate
73 immunity, facilitating its successful establishment [11]. Molecular and genetic analyses have
74 demonstrated that roots, like leaves, possess a robust innate immune system, with the
75 suppression of immunity by *P. indica* being imperative for colonisation success.
76 Investigations involving *H. vulgare* and *Arabidopsis* mutants deficient in gibberellic acid
77 (GA) and jasmonic acid (JA) metabolism, respectively, have indicated an enhanced root
78 immune response and diminished colonisation.

79
80 *P. indica* predominantly relies on JA-mediated suppression of early immune
81 responses and other defence pathways, such as salicylic acid (SA) and glucosinolate-related
82 pathway [57]. Mutants impaired in SA and glucosinolate defences exhibit increased
83 susceptibility to *P. indica*. The disruption of endoplasmic reticulum (ER) integrity by *P.*
84 *indica* potentially interferes with the secretion of immunity-associated proteins, suppressing
85 immune signalling and facilitating colonisation. With the genome of *P. indica* now available,
86 the possibility of identifying effector molecules targeting immune signalling components
87 exists.

88 **Plant Interaction and Calcium Ions**

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91 Mutualistic and commensal relationships in fungi exhibit parallels during their initial
92 infection and colonisation phases [22]. Understanding the mechanisms of recognition and
93 early signalling is imperative for plants to discern between beneficial and detrimental
94 microbes that impact plant physiological processes. Upon recognising these symbionts, there
95 is a rapid surge in intracellular calcium levels, marking an early signalling event. Calcium
96 ions function as secondary messengers in diverse plant signalling pathways, influencing plant
97 responses [5]. Autoclaved cell wall extract from *P. indica* induces calcium elevation and
98 fosters growth in various plant species. The significance of root colonisation is underscored
99 by autoclaved cell wall extract induced calcium elevation in roots [20].

101 At the interface between plants, *P. indica* engages in signal exchange that modulates
102 phosphorus influx and calcium efflux within plant cells. These signals originating from
103 endophytes can initiate programmed cell death or stimulate growth and development via
104 phytohormones [38]. Plants with mutations impairing gibberellic acid (GA) and jasmonic
105 acid (JA) metabolism exhibit decreased colonisation and inhibited growth [40]. During
106 programmed cell death (PCD), calcium and phytohormones regulate gene expression, with *P.*
107 *indica* colonisation resulting in DNA fragmentation and cell shrinkage [41]. Structural
108 alterations in Arabidopsis roots during cell death associated with *P. indica* colonisation may
109 stem from the induction of endoplasmic reticulum (ER) stress and suppression of the
110 unfolded protein response (UPR) [47].

111 **Genome Level**

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114 During the colonisation of Arabidopsis roots, *P. indica* undergoes a biotrophic phase
115 followed by cell death, ultimately not leading to any disease symptoms. *P. indica* utilises
116 these deceased cells for intracellular sporulation. Analysis of colonised *H. vulgare* roots has
117 unveiled distinctive gene regulation during various stages of colonisation, with numerous
118 genes induced by symbiosis being specific to *P. indica* [58]. Plant hormones such as jasmonic
119 acid (JA) and ethylene are released from root prime shoots to enhance disease resistance [9].
120 In combating powdery mildew fungus, up-regulation of JA and ethylene signalling pathways,
121 rather than salicylic acid (SA) signalling, is observed [39].

122 **Programmed Cell Death**

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124
125 In general, plant-programmed cell death (PCD) represents a natural reaction to
126 various physiological challenges triggered by internal or external stimuli. It constitutes a
127 metabolically regulated mechanism pivotal for plant development. Plant PCD resembles
128 animal apoptosis, encompassing chromatin condensation, cell shrinkage, and DNA
129 fragmentation [13]. The colonisation of roots by fungi entails both a biotrophic growth phase
130 and a phase-dependent on cell death. Previous investigations into *P. indica* colonisation in
131 plant roots indicates a comparable pattern of biotrophic and cell death-dependent phases,
132 potentially employed by the fungus for intracellular sporulation [17]. In contrast to pathogen-
133 induced HR, cell death was observed during *P. indica* colonisation might not signify a robust
134 plant defence response, as suggested by the feeble and transient upregulation of defence
135 marker genes.

136
137 Transmission electron microscopy has revealed that cells remain viable during fungal
138 penetration, undergoing structural modifications as colonisation progresses [31]. This implies
139 that fungal colonisation entails more than merely targeting diseased cells. Although host cells
140 ultimately perish upon colonisation, the strategy does not solely rely on the presence of dead
141 cells. Evidence indicates that the colonisation process is contingent upon host cell demise, as
142 demonstrated by the diminished colonisation of roots in plants overexpressing the negative
143 cell death regulator BI-1. Moreover, the ER plays a crucial role in processing immunity-
144 related proteins, including the pattern recognition receptor. *P. indica* induces ER stress in
145 roots, inhibiting the unfolded protein response pathway (UPR) while initiating a pro-
146 apoptotic signalling cascade due to the incapacity of colonised cells to alleviate ER stress.
147 Vacuolar collapse is essential for *P. indica*-induced cell death and root colonisation,
148 facilitated by vacuolar processing enzymes (VPEs). Arabidopsis mutants lacking VPEs
149 exhibit decreased fungal colonisation, emphasising the significance of vacuolar collapse in
150 cell death and colonisation [18]. *P. indica* employs a two-phase colonisation strategy

151 involving biotrophic adaptation and ER stress-induced caspase-dependent vacuolar cell death
152 for successful symbiosis with *Arabidopsis* [17].

153

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

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163 **Seed Germination, Growth and Development**

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165 *Piriformospora indica* has substantially improved growth and yield across various
166 crops, horticultural specimens, and medicinal plants. Its presence promotes seed germination,
167 development, and productivity while enhancing viability even in unfavourable environments .
168 Additionally, it facilitates early germination in vascular plants and influences seed-oil yield in
169 *Helianthus annuus* [53]. Colonisation of plant roots by *P. indica* has been associated with
170 increased seed yield in various plant species [51]. In medicinal plants, its presence is deemed
171 essential for enhancing the production of chemical compounds and secondary metabolites.
172 *P. indica* has been found to boost the production of anticancer drugs and overall biomass
173 productivity in diverse plant species. Furthermore, *P. indica*-mediated enhancements have
174 been observed in the growth and biomass of various crop plants . Its ability to produce auxin
175 stimulates root growth and influences gene expression differentially across different plant
176 species [57]. Additionally, it stimulates the synthesis of secondary metabolites, such as
177 pentacyclic triterpenoids, in suspension cultures of certain plants [35]. Overall, *P. indica*
178 demonstrates potential as a biopriming agent for augmenting plant biomass growth
179 [32]. Researchers at Kerala Agricultural University conducted experiments utilising a growth
180 medium containing *P. indica* fungus mixed with various components to improve nutrient
181 utilisation efficiency in rice cultivation. The most effective blend, consisting of paddy soil,
182 farmyard manure (FYM), and coir pith compost in equal proportions, significantly enhanced
183 rice seedling growth compared to standard conditions [2,3].

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185 **Plant Growth Promotion**

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

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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 [57]. 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 [21]. *P. indica* fosters growth by effectively transporting, absorbing, and mobilising nutrients from the soil, encompassing nitrogen, phosphorus, potassium, sulphur, magnesium, iron, zinc, manganese, and copper. 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 [12]. The fungus demonstrates adeptness in utilising various phosphate sources, underscoring its role as both a mobiliser and a solubiliser of phosphorus in soil.

Increased Photosynthetic Efficiency

Various chlorophyll (Chl) content and fluorescence parameters indicate plant health and photosynthetic activity. Plants inoculated with *P. indica* exhibited elevated levels of Chla and carotenoids [16]. Furthermore, in *Arabidopsis*, colonisation by *P. indica* resulted in increased electron flow in PSII and heightened levels of both photochemical and non-photochemical quenching [23]. Colonization by *P. indica* had a notable impact on tiller production, resulting in an increase of 10.64%, 16%, and 15.69% at 30, 45, and 60 days after transplanting (DAT) respectively, compared to non-colonized plants. Additionally, colonized plants subjected to irrigation with 30 mm cumulative pan evaporation to a depth of 3 cm exhibited the highest leaf area index (4.54) at 60 DAT and dry matter production (4559.26 kg ha⁻¹) at harvest [28].

Modulating Phytohormone Levels

Plant hormones such as auxin, cytokinin, ethylene, abscisic acid, and gibberellins are indispensable in regulating plant growth and organ development [44]. These hormones significantly influence growth in plant species like *Arabidopsis*, barley, and Chinese cabbage when influenced by the presence of *P. indica* [57]. Promoting growth in Chinese cabbage and barley correlates with heightened levels of auxin and gibberellins in the roots colonised by the fungus. 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. The intricate interplay of diverse phytohormones and their signalling networks is pivotal for establishing compatible endosymbiosis between *P. indica* and plants [38].

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 [1].

251 Plants significantly influence the microbial communities in the soil, particularly in the
252 rhizosphere, through carbon input via root exudates. Due to their immobility, plants
253 encounter challenges such as nutrient scarcity, salinity, drought, and pathogen attacks,
254 leading them to form associations with beneficial microorganisms to alleviate these stressors.
255 Symbiosis with beneficial fungi assists in nutrient acquisition by plant roots, enhancing soil
256 fertility and crop yield. Similarly, endophytic fungi like *P. indica*, akin to mycorrhizal
257 endosymbionts, have been recognised as growth enhancers for various plant species. Rice
258 plants colonized with *P. indica* exhibited increased nutrient absorption under both stressful
259 and non-stressful conditions. In contrast, non-colonized plants displayed the lowest uptake of
260 NPK nutrients, especially under conditions of very severe and extremely severe stress. The
261 beneficial impacts of endophytic colonization with *P. indica* were apparent in the modified
262 root structure, showcasing increased root volume, length, and depth in summer rice [30].
263

264 *P. indica* improves plant growth in Arabidopsis by facilitating the absorption of
265 phosphorus (P) from the soil [6]. The PiPT gene, essential for phosphate transportation, is
266 identified in plants colonised by *P. indica* [33]. Furthermore, *P. indica* triggers the expression
267 of phosphate transporters in Arabidopsis and mung bean plants, resulting in elevated levels of
268 nitrogen (N), phosphorus (P), and potassium (K) [43]. The interaction between the fungus
269 and the roots induces changes in protein composition, enhancing the expression of enzymes
270 involved in nutrient assimilation. Additionally, nitrogen uptake and assimilation are enhanced
271 by *P. indica* colonisation, with increased nitrate reductase activity observed in Arabidopsis
272 and tobacco roots [24]. In contrast to arbuscular mycorrhizal fungi (AMF), *P. indica* promotes
273 nitrate uptake rather than ammonium [15]. *P. indica* also facilitates the mobilisation of
274 micronutrients from the soil, thus supporting plant growth and development [6].
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276 **Phosphorus Acquisition**

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278 Phosphorus (P), an essential mineral nutrient, constitutes approximately 0.5% of the
279 dry weight of plant cells and serves various functions in regulation, structure, and energy
280 transfer. Plants encounter difficulties accessing soil P primarily due to its predominantly
281 insoluble form, which impedes crop production globally [8]. They acquire P through direct
282 uptake and associations with mycorrhizal fungi. Colonization by *P. indica* boosted the
283 absorption of phosphorus from the soil into the plant, leading to the growth of an extensive
284 root system characterized by increased volume [29]. *P. indica* facilitates the uptake and transfer
285 of P to the host plant through an energy-dependent process, which involves the production of
286 acid phosphatases aiding in the access of insoluble P reserves. While high-affinity phosphate
287 transporters have been identified in various plant and fungal species, the lack of stable
288 transformation systems in arbuscular mycorrhizal (AM) fungal species poses a challenge to
289 understanding [14]. The functional characterisation of a phosphate transporter in *P. indica*
290 underscores its significance in transporting phosphorus to the host plant. However, the
291 transfer mechanism remains ambiguous, hypothesised to occur at the interface between the
292 plant and fungus, necessitating the involvement of two transporters [56].
293

294 Participation of *P. indica* in phosphate transfer and its role in enhancing host plant
295 growth exhibit discrepancies. *P. indica* enhances phosphate uptake and promotes *Arabidopsis*
296 growth akin to mycorrhizal fungi [6]. The involvement of *P. indica* in phosphate transfer to
297 *Zea mays* was evidenced, suggesting a molecular mechanism involving PiPT. However,
298 despite an increase in grain yield independent of phosphorus and nitrogen levels, no
299 discernible improvement in phosphate supply was noted in the *P. indica*-*Hordeum vulgare*
300 symbiosis. Phosphate levels significantly influenced *Z. mays* biomass when colonised by *P.*

301 *indica*. Moreover, growth promotion of *P. indica* was more pronounced under low phosphate
302 conditions, indicating its potential for enhancing crop productivity in phosphate-deficient
303 soil. The phosphate transfer mechanism from *P. indica* to plants remains partially understood,
304 with hypotheses proposing cytoplasmic streaming or bulk flow through external hyphae.

305
306 A more extensive array of host plants is required to determine whether *P. indica* and
307 PiPT demonstrate host specificity. Using *P. indica* and PiPT can bolster crop enhancement
308 efforts and serve as a model for investigating molecular mechanisms and plant phosphate
309 uptake [17]. The strategy of *P. indica* for root colonisation involves programmed cell death,
310 suggesting that phosphate released into deceased cells could be assimilated by neighbouring
311 living cells and distributed throughout the plant.

312 **Gene Regulator and Mineral Uptake**

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315 The fungus facilitates nitrate/nitrogen absorption in plants and modulates source-sink
316 relationships by increasing the expression of specific genes. Plants hosting *P. indica* exhibit
317 elevated rates of CO₂ assimilation, consequently promoting additional sinks in a balanced
318 manner. Moreover, *P. indica* colonisation has been linked to increased N, P, and K levels in
319 chickpeas and black lentils while mitigating Fe and Cu deficiencies in sugarcane (Liu *et al.*,
320 2020). The presence of the receptor kinase in *Arabidopsis* roots undergoes modification upon
321 colonisation, leading to enhanced uptake of labelled phosphorus [46]. This mutualistic
322 interaction fosters plant growth and development by influencing diverse regulatory and
323 structural processes and facilitating energy transfer. Additionally, a reduction in phosphate
324 content was observed in maize plants colonised by a *P. indica* mutant lacking a phosphate
325 transporter.

326 **Reactive Oxygen Species Modulation**

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329 *Piriformospora indica* has been demonstrated to enhance stress tolerance in various
330 crops, including barley, wheat, maize, tomato, and lentil, by augmenting phosphate uptake
331 through elevated levels of alkaline phosphatase and acid phosphatase enzymes in the
332 rhizosphere [6]. Research indicates that *P. indica* enhances stress tolerance in wheat, barley,
333 and maize by regulating reactive oxygen species (ROS) generation and antioxidant defence
334 pathways. ROS generation and defence-related responses are initially activated during the
335 early stages of mycorrhizal associations but diminish after establishing the symbiotic
336 relationship [49]. Hydrogen peroxide triggers defence responses, yet its production is
337 suppressed in *P. indica*-colonized roots under favourable conditions, promoting growth
338 response [50]. Initially, exudates from *P. indica* induce ROS generation and accumulation of
339 stress-responsive hormones, but upon physical contact, defence responses decrease, and
340 stomata reopen [54]. This interplay between ROS generation, scavenging, signalling, and
341 mycorrhizal association ultimately enhances plant resilience under stress conditions.

342 **Drought tolerance**

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345 Extensive research has been conducted on *P. indica* due to its ability to bolster crop
346 resilience against various abiotic stresses, including salinity, low temperature, and heavy
347 metal toxicity. [4] concluded that *P. indica* could improve chlorophyll level under severe water
348 stress situations in contrast to the fungus non-inoculated water-stressed plants. *P. indica*
349 colonized plants under drought stress showed higher chlorophyll content (0.07g L⁻¹) and
350 proline (20.9 µg mL⁻¹) thereby, improved water uptake from water deficit soil and escaped

351 adverse effects of water stress. [52] reported that *P. indica* colonized plants irrigated at 35
352 mm CPE to a depth of 3 cm resulted in taller plants. However, *P. indica* colonized plants both
353 under ideal non stressed condition (irrigation interval at 30 mm CPE to a depth 3 cm) and
354 severe stress condition (irrigation interval at 40 mm CPE to a depth 1.5 cm) resulted in taller
355 plants than non-colonized/ control plants at the same degree of stress. This indicated that the
356 detrimental effect of moisture stress on plant height was counteracted by *P. indica*
357 colonization. The adverse effects of moisture stress could be substantially reduced through the
358 advantageous relationship between rice and the root endophyte *P. indica* in rice. Colonization
359 additionally improved the water use efficiency of rice by 29% in comparison to non-colonized
360 plants under severe stress, an effect influenced by both root spread and volume [30].

361

362 **Salinity tolerance**

363 It has been documented to enhance tolerance to high salinity in *Triticum aestivum*
364 and drought stress in *Arabidopsis* seedlings, Chinese cabbage, and strawberries [17]. The
365 presence of *P. indica* has been associated with the activation of defence-related genes, genes
366 responsive to abiotic stress, and osmoprotectants. Moreover, *P. indica* has evolved
367 mechanisms to deliver effectors intracellularly to facilitate microbial infection and influence
368 host metabolism. These effectors are pivotal in initiating and perpetuating symbiosis,
369 enabling the fungus to manipulate the plant's defence mechanism. Specific proteins such as
370 PIIN_08944 have been identified among these effectors, aiding plant colonisation by
371 suppressing the salicylate-mediated basal resistance response [45]. Expression of PIIN_08944
372 in *Arabidopsis thaliana* and *Hordeum vulgare* has been shown to dampen the activation of
373 immune pathways elicited by flg22, impacting pattern-triggered immunity (PTI) and the
374 salicylic acid (SA) defence pathway. PIIN_08944 facilitates root colonisation by *P. indica* by
375 interfering with the host plant's basal immune responses [48]. Additionally, *P. indica* has been
376 observed to modulate antioxidant defence enzymes and other components of the ROS-
377 scavenging system, thereby enhancing plant tolerance to various stresses and providing
378 protection against pathogens [7].

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380 **Tolerance to biotic stresses**

381 *Piriformospor indica* is pivotal in safeguarding plants against diverse biotic stresses,
382 such as fungi, bacteria, and viruses. Upon encountering pathogens, this fungus triggers the
383 upregulation of defence-related genes in host plants, including pathogenesis-related genes
384 and those involved in jasmonate and ethylene signalling [36]. Furthermore, the colonisation of
385 roots by *P. indica* induces systemic resistance against leaf pathogens across various plant
386 species, as evidenced by the elevation of defence-related gene expression [37]. The fungus *P.*
387 *indica* demonstrates promise in bolstering plant resistance against fungal diseases. Plants
388 treated with *P. indica* also defend against *Fusarium culmorum* and *Blumeria graminis*.
389 Additionally, *P. indica* has proven effective in biocontrol against *T. aestivum* and lentil
390 diseases caused by various pathogens.

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392 Greenhouse experiments involving *T. aestivum* have shown reduced leaf, stem, and
393 root disease incidence upon colonisation with *P. indica*. Moreover, *P. indica* enhances
394 resistance to powdery mildew in *Arabidopsis* through JA signalling and positively modulates
395 plant defence responses. The establishment of *P. indica* within plant hosts triggers the
396 activation of the antioxidant system, thereby bolstering crop resilience against diverse
397 stressors [6]. *P. indica* exhibits bio-protection against numerous pathogens in wheat and
398 maize and the synthesis of secondary metabolites as natural pesticides [19]. The interaction
399 between *A. thaliana* roots and *P. indica* prompts ethylene production, influencing the stability
400 of advantageous traits. Ethylene also facilitates *P. indica* colonisation of plant roots through

401 signalling mechanisms, underscoring the significance of ethylene signalling in establishing
402 symbiosis between the fungus and the host plant.

403

404 **Conclusion**

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406 *Piriformosporaindica*, demonstrates remarkable adaptability as it manipulates the
407 hormonal signals to fortify their defences against fungal and viral maladies. Within plant
408 system, it assumes multifaceted roles: an adept extractor of nutrients, a protector against
409 diseases, against stresses, orchestrating the progress of growth. Its presence within the
410 medicinal flora produce secondary metabolites, casting a spell of both commerce and
411 biotechnology. *P.indica* stands as an organism embodying traits of both the symbiotic and the
412 saprophytic.

413

414 **COMPETING INTERESTS**

415 Authors have declared that no competing interests exist

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417 **References**

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