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45 **INTRODUCTION**

46 The world population has increased very rapidly in the last century, from 1.6 billion people
47 in 1900 to 7.0 billion in 2011. In this sense, it is estimated that the world population will
48 reach 9.7 billion in 2050, with a resulting increase in the demand for resources, such as water
49 (Le Cocq et al., 2017). Given this scenario, food production will need to increase by roughly
50 70% by 2050 and double or triple by 2100, while trying to decrease the environmental impact

51 of the food production activity (Crist et al. 2017; Poveda, 2021a). Therefore, the development
52 of environmentally sustainable agriculture is necessary, where biofertilizers, biostimulants
53 and biopesticides must play a fundamental role.

54 Plant-pathogen microorganism interactions have a negative impact on the productivity of
55 main agricultural crops. However, there is a wide range of microorganisms whose interaction
56 with plants could be beneficial, like for example, endophytes (Mei & Flinn, 2010).
57 Etymologically, the term 'endophyte' means 'inside the plant' (*endon*: within, *phyton*: plant),
58 whose classical definition indicates that endophytes are fungi or bacteria which, for all or
59 part of their life cycle, invade the tissues of living plants and cause unapparent and
60 asymptomatic infections entirely within plant tissues but cause no symptoms of disease
61 (Wilson, 1995).

62 It has been estimated that there are approximately 1 million endophytic fungal species
63 distributed across all ecosystems, from hot deserts to tropical forests, and they may colonize
64 roots, stems, and/or leaves (Lugtenberg et al. 2016). Endophytic fungi play an important role
65 in the physiology of host plants, since this association may have protective effects on these
66 plants. The presence of these microorganisms may suppose an increasing resistance to biotic
67 stresses for the plants, due to production of metabolites, such as alkaloids, mycotoxins and
68 antibiotics, the induction of antimicrobial or immunological compounds production by
69 plants, or simply, by space competition with these pathogens. Furthermore, these benefits
70 also include an increase in the plant tolerance to stressful factors, such as salinity, drought,
71 heavy metal presence or low pH (Yan et al. 2019; Poveda, 2020a).

72 However, one of the most interesting benefits of the endophytes is the host growth promotion.
73 All the mechanisms described above enhance plant growth promotion (PGP) indirectly, but
74 there are a wide variety of mechanisms that play an important role in PGP directly by
75 improving plant nutrition, thanks to, for example, the endophytes' production of compounds
76 like vitamins (Yan et al. 2019), phytohormones such as indole-3-acetic acid (IAA)
77 (Contreras-Cornejo et al. 2009), and secondary metabolites (Kusari et al. 2012). This
78 improvement can also occur through an increasing supply of water (Hosseini et al. 2016), as
79 well as the solubilization of nutrients present in the soil such as phosphorus, among others
80 (Zabalgogezcoa et al. 2006) or through production of siderophores (Ripa et al. 2019). These,

81 and other mechanisms, will be covered in depth throughout this review. Comprehension of
82 all these mechanisms described above represents a very useful tool for the advance of more
83 productive sustainable agriculture. Thanks to their potential to promote plant growth, the use
84 of endophytic fungi could be a promising tool to increase crop yield and reduce the
85 dependence on these agrochemicals, in the context of sustainable agriculture (Diene &
86 Narisawa, 2009). The use of biofertilizers can help to reduce the use of these chemicals, since
87 they improve the nutrient supply and their availability in the soil thanks to their biological
88 activity, that is, through nitrogen fixation, phosphate and/or potassium solubilization, or the
89 release of plant growth regulating substances, among others. In addition, their use would help
90 to reduce the loss of nutrients from chemical fertilizers, since only between 10% and 40% of
91 the total is finally taken up by plants, the rest being leached (Pal et al. 2015).

92 Among the microorganisms used as biofertilizers, one of the most important group at an
93 economic level is the species of the *Epichloë* genus, which are endophytic fungi that establish
94 associations with the aboveground tissues of cool-season grasses (Kauppinen et al., 2016).
95 For example, Wang et al. (2019) showed how, under high salt conditions, endophyte *Epichloë*
96 *bromicola* increased the tolerance of wild barley (*Hordeum brevisubulatum*) to this stress by
97 increasing seed germination and growth capacity, endophytic fungi considered a model
98 organism for investigating aspects of endophytic biology, as well as exploring the ecological
99 implications and molecular bases of symbiosis (Lugtenberg et al. 2016). Another example of
100 an endophyte with high economic importance is *Piriformospora indica*, which forms
101 symbiosis with a broad host range, including important crops like *Hordeum vulgare*, and
102 model plants like *Nicotiana tabacum* and *Arabidopsis thaliana* (Lugtenberg et al. 2016).

103 However, the efficient use of these microorganisms requires broadening the knowledge of
104 aspects such as the stability of the symbiosis and the specificity of the host, as well as the
105 characterization of chemical compounds produced by these microorganisms which can have
106 numerous applications (Diene and Narisawa 2009). As far as specificity of the host is
107 concerned, it is known that there are endophytic fungi, like *Neotyphodium* (anamorphs of
108 *Epichloë*), that are specific to cool season grasses only; therefore, their application in crops
109 is very limited (Karimi et al. 2012). However, there are other endophytic fungi that show
110 little or no host specificity, like dark septate endophytes, being able to be widely used in

111 agriculture (Hidayat 2019). Along with this, it is important to thoroughly analyze the stability
112 of the symbiosis for each specific interaction. Plant endophytic fungi do not cause disease
113 symptoms in their hosts; however, under adverse environmental conditions, some fungi can
114 behave as pathogens as a survival strategy. This happens with fungal species such as
115 *Phialocephala fortinii* or *Leptodontidium orchidicola*, which present drawbacks for their
116 widespread use in agriculture (Diene and Narisawa 2009). There are pathogenic fungi that
117 can behave as beneficial endophytes under certain environmental conditions and hosts, such
118 as the *Sclerotinia sclerotiorum* necrotroph in cereals (Tian et al., 2020) due to being infected
119 by mycovirus (Zhang et al., 2020).

120 In order to establish themselves in host tissues, endophytic fungi (yeasts and filamentous
121 fungi) must overcome host resistance. According to Schulz et al. (2015), endophytes do so
122 through different mechanisms, which may or may not be combined: secretion of lytic
123 enzymes and metabolites that are toxic to their hosts, modulation of host phytohormones,
124 such as jasmonic or salicylic acids and detoxification of constitutive host defence metabolites
125 (Schulz et al. 2015), such as glucosinolates (Poveda, 2021b).

126 Multiple factors affect the outcome of the plant-endophyte interaction, both from the agents
127 involved and from the environment. From the first moment of the interaction, there is an
128 important plant-fungus molecular dialogue that regulates the gene expression of both
129 organisms to achieve effective colonization. Any change in the gene expression of the fungus
130 or the plant may cause the fungus to start behaving like a pathogen (Müller & Krauss, 2005;
131 Moricca & Ragazzi, 2008; Aly et al. 2011). Environmental factors such as temperature or
132 gaseous regimes also affect this interaction (Hendry et al. 2002), which could be related to
133 the increase in the incidence, diversity and host breadth of endophytes as a function of
134 latitude that previous authors had shown (Arnold, 2007; Arnold & Lutzoni, 2007; Aly et al.
135 2011). Environmental conditions also affect the distribution pattern of endophytic fungi
136 (Suryanarayanan et al. 2005; Song et al. 2007).

137 Endophytic fungi can be divided into two main groups - yeasts and filamentous fungi, which
138 may use different mechanisms to promote plant growth.

139 **ENDOPHYTIC FILAMENTOUS FUNGI AND YEASTS**

140 Endophytic filamentous fungi may be transmitted either vertically (via seeds) or horizontally
141 (Lugtenberg et al., 2016). In the case of vertical transmission, the fungus grows into the
142 embryo of a developing seed and, during the germination of the seed it colonizes it
143 (Lugtenberg et al., 2016). Colonisation by horizontally transmitted endophytic filamentous
144 fungi follows a sequence that starts with fungi recognising the potential host, for example,
145 by lectin-like molecules, as in *Hypoxylon fragiforme* on beech (Chapela et al., 1993). Then
146 comes the spore germination, then the fungal endophyte may penetrate the host through the
147 epidermis or through other means (natural wounds), and finally follows the tissue
148 colonization, as it happens, for example, in *Alnus* colonization by *Melanconium* (Sieber et
149 al., 1991). Once they are inside the host plant tissues, some fungal endophytes may assume
150 a quiescent (latent) state for a period of time that may extend for the whole lifetime of the
151 host, or until environmental conditions are favourable for the fungi to reverse to its previous
152 state (Nisa et al. 2015, Jia et al. 2016).

153 Endophytic filamentous fungi may give their host plants protection against biotic stressors
154 by producing antagonistic secondary metabolites such as alkaloids, competing with them for
155 space, inducing plant resistance, stimulating plant secondary metabolites or promoting plant
156 growth and physiology (Rai et al. 2014; Poveda et al. 2020a). Also, many fungal
157 entomopathogens such as *Metarhizium*, *Beauveria* or *Isaria* are capable of colonizing plants
158 as well (Vidal & Jaber 2015; Lugtenberg et al. 2016). Endophytic filamentous fungi have
159 been shown to confer tolerance for abiotic stress to host plants, including extreme
160 temperatures, salinity, drought or presence of heavy metals in soil (Aly et al. 2011; Rodriguez
161 et al. 2012; Waqas et al. 2012). The proposed mechanisms are the induction of a high
162 antioxidant environment for detoxifying ROS released upon stress (Johnson et al. 2014;
163 Lugtenberg et al. 2016), production of phytohormones such as gibberellic acid (GA) (Khan
164 et al. 2011; Bilal et al. 2018), or enhancing nutrient acquisition (Yan et al. 2019). Regarding
165 tolerance to heavy metals, many endophytic fungi have degradation pathways, metal
166 sequestration or chelation systems that help reducing the impact of these toxic components
167 on plants, thus helping host plants survival in contaminated environments (Aly et al. 2011;
168 Deng & Cao, 2016).

169 Endophytic filamentous fungi may also play the ecological role of saprobes, since they
170 initiate the biological degradation of a dead or dying host plant and thus nutrient recycling
171 (Boberg et al. 2011; Lugtenberg et al. 2016). Previous authors have speculated that, in order
172 to transition from endophyte to saprobe lifestyle, sporulation after host senescence is required
173 for some species to complete their life cycle (Vazquez de Aldana et al. 2013). On the other
174 side of this interaction, endophytic fungi obtain spatial structure, protection from desiccation
175 and a source of nutrients from plants and, in the case of vertical transmission, also
176 dissemination to the next generation of hosts (Rudgers et al. 2004; Aly et al. 2011).

177 Endophytic yeasts are unicellular fungi that reside within plant tissues for part of their life
178 cycle without causing any apparent damage to them (Petrini 1991). This endophytes group
179 includes both commensal microorganisms with no direct effect on their host, and plant-
180 beneficial microorganisms (Sturz et al. 2000; Nassar et al. 2005).

181 Most endophytic yeast cells penetrate the plant through stomata, cuticles, epidermis and
182 mechanical microdamage, but without causing direct damage. However, some species show
183 enzymatic activities that enable these cells to penetrate internal plant tissues through local
184 damage, such as cell-wall degrading enzymes or cutinases (Paungfoo-Lonhienne et al. 2010;
185 Doty, 2013). After penetrating the plant, yeasts reproduce both in the intercellular and
186 intracellular space of vegetal tissues (Isaeva et al. 2010). Many endophytic yeasts have been
187 isolated directly from plant tissues, including genera *Cryptococcus*, *Debaryomyces*,
188 *Sporobolomyces*, *Rhodotorula*, *Williopsis* and *Pichia* (Nakamura et al. 1995; Doty, 2013;
189 Nassar et al. 2005).

190 Yeasts are found in a smaller number than bacteria or filamentous fungi in soil (Phaff et al.
191 1978; El-Tarabily & Sivasithamparan, 2006). Rhizosphere is the zone where the majority of
192 yeast population is found, because yeasts assimilate the simple organic compounds related to
193 root exudates (Botha, 2006; 2011). Yeasts are not known as primary degraders of complex
194 polymers and also have to compete with other rhizosphere microorganisms, so they
195 developed symbiosis as a suitable strategy to survive (Botha, 2011). Therefore, the
196 endophytic trait offers an advantage in competition, protecting them both from other biotic
197 agents, and from abiotic conditions, and it also offers a means for obtaining nutrients directly
198 from plants (Botha, 2011).

199 Soil yeasts take part in many ecological functions, such as mineralization of organic material
200 through fermentation or respiration, nutrient transformation and solubilization, modification
201 of soil structure, plant growth promotion and plant protection against many soil pathogens
202 (Botha, 2011). Many studies have shown that plants receive other beneficial effects than
203 direct growth promotion from the interaction with certain endophytic yeasts, such as
204 protection against pathogens or the enhancement of abiotic stress tolerance (Hallmann et al.
205 1997; Stone et al. 2000; Sturz et al. 2000; Narisawa et al. 2004; El-Tarabily &
206 Sivasithamparam, 2006; Joubert & Doty, 2018). The mechanisms by which endophytic
207 yeasts protect plants against pathogens include production of antibiotics and fungal cell wall
208 degrading enzymes, such as chitinase or cellulase, and production of siderophores, which are
209 chelating molecules that inhibit pathogens by reducing available iron from their environment
210 (Chaiharn et al. 2008, Wang & Chi, 2009; Nutaratat et al. 2014).

211 **PLANT GROWTH PROMOTION MECHANISMS IN ENDOPHYTIC FUNGI**

212 In addition to the different indirect mechanisms shown so far (increased tolerance against
213 abiotic stresses, increased resistance to biotic stresses, etc.), endophytic fungi can play a
214 fundamental role in the correct development of sustainable agriculture thanks to their ability
215 as PGP. The ability of different endophytic fungal species to promote plant growth is based
216 on well-known and specific mechanisms, such as the increase in nutrient acquisition, the
217 production of plant hormones, the ethylene amount reduction and the water acquisition
218 increase. A schematic classification of the fungal species identified, the crops and the
219 mechanisms involved in increasing plant growth is shown in Table 1. Despite this, there are
220 fungal species that are known for their ability to promote growth, although the exact
221 mechanism has not yet been identified in many agricultural crops.

222 *Beauveria bassiana* is a well-known fungus used in biocontrol due to its powerful
223 entomopathogenic capacity, which has been studied as an endophytic fungus in recent years.
224 In *Phaseolus vulgaris* plants, it has been described that *B. bassiana* is capable of significantly
225 increasing their growth, while the mechanisms involved are still unknown (Afandhi et al.
226 2019). *Pochonia chlamydosporia* is also a fungus that is widely used in biocontrol for its
227 nematogenous capacity and has been shown to be able to promote growth of both roots and
228 shoots of tomato plants, as well as manageroot-knot nematode infestations (*Meloidogyne*

229 *javanica*) (Escudero et al. 2012). *Trichoderma asperellum* is a fungal species also used in
230 biocontrol for its ability to parasitize pathogenic fungi and nematodes, whose presence in
231 *Sorghum bicolor* roots has been reported to significantly increase seed vigor and yield under
232 greenhouse and field conditions (Rajini et al. 2020).

233 PGP mechanisms of some species of endophytic fungi are known for various crops, but they
234 are not specifically known for others. *Serendipita indica* (= *Piriformospora indica*) is an
235 endophytic fungus that is widely studied in interaction with model plant *Arabidopsis*
236 *thaliana*, whose presence in roots of *Vigna mungo* significantly increases the dry weight of
237 roots and stems, both in isolation and in combination with rhizobacteria fluorescent
238 pseudomonads (Kumar et al. 2012). In the case of grasses, genera *Neotyphodium* and
239 *Epichloë* include various species studied and used as PGP. In *Lolium multiflorum*, the
240 presence of *Neotyphodium* sp. endophytely causes plants to produce significantly more
241 vegetative tillers and allocate more biomass to roots and seeds (Vila - Aiub et al. 2005). Or
242 in carrots, where the presence of *Epichloë trembladerae* in roots increases plant growth and
243 modifies radicular exudates, thus promoting symbiosis with arbuscular mycorrhizal fungi
244 (Vignale et al. 2018).

245 Other fungal genera include numerous crop pathogenic species that can behave like
246 endophytic fungi, depending on the host plant. In maize roots, the presence of *Phoma* sp.,
247 isolated from *Tinospora cordifolia* and *Calotropis procera*, produces a significant increase
248 in the plant growth (Kedar et al. 2014). Meanwhile, in cucumber, root endophytic fungus
249 *Fusarium equiseti* enhances the shoot dry weight of plants and significantly increases the
250 percentage of protection against anthracnose (*Colletotrichum orbiculare*) and damping-off
251 (*Rhizoctonia solani*) (Saldajeno et al. 2011); growth promotion was also observed in pea,
252 along with a suppression of root rot disease caused by *Fusarium avenaceum* and
253 *Peyronellaea pinodella* (Šišić et al. 2017). *Gaeumannomyces cylindrosporus* is a dark septate
254 endophytic fungus, isolated from Pb-Zn mine tailings soils, whose presence in maize plants
255 has been seen to increase its photosynthetic rate and plant biomass (Yihui et al. 2017).

256 As far as yeasts are concerned, there are also examples of PGP species whose specific
257 mechanisms in certain crops are still unknown. For example, in sugar beet, endophytic root
258 yeasts *Candida valida*, *Rhodotorula glutinis* and *Trichosporon asahii* are able to promote

259 plant growth and reduce damping-off, crown and root rots by pathogen *Rhizoctonia solani*
260 (El-Tarabily, 2004).

261 **Nitrogen acquisition**

262 Endophytic microorganisms have the capacity to transfer nitrogen to their plant hosts from
263 decaying organic matter in soil, in addition to increasing the nitrogen uptake efficiency in
264 nitrogen-depleted soils. It should be noted how endophytic insect-pathogenic fungi (EIPF)
265 are able to transfer insect-derived nitrogen into different plant species, converting nitrogen
266 to ammonium within the intraradical mycelia and transferring into plant roots in this form
267 (Behie & Bidochka., 2014).

268 Nitrogen transfer

269 The direct transfer of N to the plant through the formation of ammonium is mainly found in
270 cereals. In wheat, the presence of *Aspergillus niger* within roots increases plant growth thanks
271 to the formation and transfer to the plant ammonia, in the same way as it has been verified
272 with *Trichoderma harzianum* (Ripa et al. 2019) and with *T. gamsii*, in maize and legumes
273 such as soybean and lentil (Rinu et al. 2014). Also in maize, the increase in plant growth has
274 been verified by the formation of ammonia due to the root presence of *Penicillium*
275 *chrysogenum* and *P. crustosum* (Hassan et al. 2017), occurring a higher shoot and root length,
276 and fresh and dry plant biomass in the case of *Fusarium oxysporum* (Mehmood et al. 2018a).
277 In this sense, the direct transfer of N from the endophytic fungus to the plant has been verified
278 in *Brassica campestris* through dark septate endophytic fungi *Heteroconium chaetospora*, by
279 using a hydrophobic polytetrafluoroethylene membrane compartment system, which restricts
280 diffusion and mass flow of ions and allows only fungal penetration (Usuki & Narisawa,
281 2007).

282 Plant-nitrogen uptake

283 Regarding the increase in the acquisition of N by the plant thanks to the presence of
284 endophytic fungi in its organs, there are several examples of proven fungi in different crops,
285 mainly in rice. *Rhodotorula mucilaginosa* yeast, isolated from lesser bulrush (*Typha*
286 *angustifolia*), has been shown to be able to significantly increase the growth of rice plants,

287 while increasing the N content of their tissues (Paul et al. 2020). These results were observed
288 thanks to the root presence of filamentous fungus *Diaporthe liquidambaris*, promoting, in
289 turn, chlorophyll biosynthesis (Sun et al. 2019b). Also in rice, it has been proven how isolates
290 of filamentous fungus *Phomopsis liquidambari*, are able to increase the N content of plants
291 thanks to a promotion of the below-ground straw decomposition and N transformation (Sun
292 et al. 2019a). Hence, this causes an increase in the available nitrate and ammonium contents
293 in the rhizosphere soil of endophyte-infected rice under low N conditions and, in turn, an
294 increase in the potential nitrification rates, which affects the abundance and community
295 structure of the rhizospheric microbiota (Yang et al. 2015). Therefore, *P. liquidambari* in
296 rice, while improving the use of N by the plant (Li et al. 2018) and increasing its utilization
297 in nutrient-limited soil (Yang et al. 2014), is capable of modifying rhizospheric microbiota,
298 improving plant growth and development (Tang et al. 2019). In other crops such as peanut,
299 *P. liquidambari* isolated from *B. polycarpa* has also been determined to be able to increase
300 the content of vegetable N thanks to enhancing the efficiency of nodulation and nitrogen
301 fixation, by enriching the diversity of nodular endophytic bacteria (Wu et al. 2019).

302 *Metarhizium brunneum* is a filamentous fungus that is widely used as a biocontrol agent in
303 agriculture against different insect pests. In addition, it has been proven that its presence in
304 potato roots is capable of increasing the N content in plant tissues, thus increasing its biomass,
305 leaf area and the number of root forks (Krell et al. 2018a, 2018b). Similarly, filamentous
306 fungus *Xylaria regalis*, isolated from giant cedar (*Thuja plicata*), is able to increase the length
307 of stems and roots in chilli, thanks to an increase in the N content of its tissues and in the
308 synthesis of chlorophyll (Adnan et al. 2018). Even an endophytic-leaf fungi, such as
309 *Colletotrichum tropicale*, which has been isolated from leaves of *Theobroma cacao*, it is able
310 to increase N uptake and increase plant biomass (Christian et al. 2019).

311 It has been reported how different endophytic fungi are capable of degrading organic N
312 resources and increasing their plant acquisition, thus increasing their biomass, such as
313 filamentous fungus *Scolecobasidium humicola* in tomato (Mahmoud & Narisawa, 2013) or
314 dark septate endophytic fungi *Phialocephala fortinii* in *Asparagus officinalis* (Narisawa,
315 2017). On the other hand, in grass *Festuca rubra*, it has been proven that filamentous fungus

316 *Epichloë festucae* is capable of increasing N acquisition, but without significantly increasing
317 plant growth (Vázquez de Aldana et al. 2013).

318 **Phosphorus acquisition**

319 Phosphorus (P) is, after nitrogen, the second most important plant nutrient (Khan et al. 2014).
320 In this sense, the accessible P present in some soils does not supply the plants' needs for
321 soluble phosphate (Behie & Bidochka., 2014), so the microorganisms present in the
322 rhizosphere play a key role in making P available to plants from both inorganic and organic
323 sources by solubilizing. The principal strategy adopted by these microorganisms is the
324 secretion of low molecular mass organic acids (OA), which chelate mineral ions or decrease
325 the pH in order to bring P into solution. Moreover, it has also been reported how inorganic
326 acids, such as asnitric and sulphuric produced by some microorganisms increase the P
327 availability in soils (Khan et al. 2014).

328 Phosphorus solubilization

329 Different filamentous fungi with *in vitro* capacity to solubilize phosphates have also been
330 directly isolated from agricultural crops. *Penicillium sclerotiorum* was isolated from tea roots
331 (Nath et al. 2015), *Byssochlamys nivea* was isolated from *Pistacia vera* roots (Dolatabad et
332 al. 2017), and fungi *Setosphaeria rostrata*, *Ophiosphaerella* sp., *Drechslera* sp., *Curvularia*
333 sp. and *Cochliobolus* sp. were isolated from wheat roots, showing a high potential for their
334 application as biofertilizers in different soils in order to manage sustainable agroecosystems
335 (Spagnoletti et al. 2017). This mechanism is determined *in vitro* by biochemical techniques.
336 In this way, endophytic filamentous fungi from plants unrelated to agricultural crops have
337 been isolated, which could have a potential use in agriculture. Fungi *Epicoccum nigrum* and
338 *Paecilomyces variotii* could be isolated from succulent *Caralluma acutangula*, fungi with
339 phosphate solubilization capacity *in vitro* (Ali et al. 2019), in the same way that
340 *Mucoromycotina guilliermondii* was isolated from pteridophyte *Drynaria quercifolia* (Aban
341 et al. 2017), and from frankincense tree (*Boswellia sacra*) *Preussia* sp. (Khan et al. 2016), to
342 mention a few examples of fungi with potential use in agriculture, after being tested on crops.

343 Once the *in vitro* ability to solubilize phosphates of endophytic fungi was known, the
344 inoculation of different agricultural crops has reported significant increases in the nutritional
345 contribution to plants. In maize, it has been shown how filamentous fungus *Penicillium*
346 *crustosum* is able to increase plant growth through the phosphate solubilization capacity
347 (Hassan et al. 2017), as well as yeasts *Candida railenensis*, *Meyerozyma guilliermondii* and
348 *Solicoccozyma aerea* (Sarabia et al. 2018b), thanks to providing better rates of P uptake, as it
349 was verified with filamentous fungi *Aspergillus brasiliensis* and *A. sydowii* (Baron et al.
350 2018). Along with maize, this ability to promote plant growth by phosphate solubilization
351 has been determined in other crops, such as soybean, wheat and lentil by filamentous fungi
352 *Trichoderma gamsii* (Rinu et al. 2014), and in lettuce and Chinese cabbage by yeast *M.*
353 *guilliermondii*, in turn improving the seed vigor index (Nakayan et al. 2013). Also in
354 rapeseed, thanks to the phosphate solubilization, filamentous endophytic fungus *S. indica* is
355 able to promote plant growth (Wu et al. 2018); in *Asparagus officinalis*, it is done by dark
356 septate endophytic fungi *Phialocephala fortinii* (Narisawa, 2017); in cucumber, *Trichoderma*
357 *asperellum* significantly promotes seedling growth (Qi & Zhao, 2013); in wheat and lentil,
358 *Penicillium bilaiae* and *P. radicum* increase shoot growth (Wakwlin et al. 2007); and in
359 *Capsicum chinense*, *Byssochlamys brongniartii* causes an increase in the diameter of its fruits
360 (Toscano-Verduzco et al. 2020).

361 Plant-phosphorus uptake

362 Regarding the increase of plant capacity for P uptake, we find several examples in vegetable
363 crops such as *chilli*, where filamentous fungus *Xylaria regalis* isolated from *Thuja plicata*
364 increases P content of the seedling tissues, as well as the length of its stems and roots (Adnan
365 et al. 2018). In sweet basil, *S. indica* increases significantly shoot and root dry weight (Sabra
366 et al. 2018). In potato, biocontrol-fungi *M. brunneum* increases the number of root forks
367 (Krell et al. 2018a), the P content of their tissues, the leaf area and their biomass (Krell et al.
368 2018b). In maize, yeasts *C. railenensis* and *Cryptococcus flavus* significantly increase plant
369 growth in addition to shoot P content (Sarabia et al. 2017; Sarabia et al. 2018a); in wheat,
370 filamentous fungi *Trametes versicolor* and *S. indica* are capable of increasing the grain yield
371 significantly (Taghinasab et al. 2018); and in rice, *P. liquidambari* improves P acquisition
372 and utilization, also influencing the patterns of microbiota shift in the rhizosphere (Tang et

373 al. 2019). In other grass-type crops, such as *F. rubra*, *F. arundinacea* or *Lolium perenne*,
374 filamentous fungi *E. festucae*, *Neotyphodium coenophialum* and *N. lolii* have been
375 determined to increase plant growth (Zabalgogezcoa et al. 2006), together with the
376 acquisition of other nutrients (Rahman & Saiga et al. 2005) and root biomass (Ren et al.
377 2007), respectively. However, in *F. rubra*, Vázquez-de-Aldana et al. (2013) pointed out how
378 *E. festucae* is capable of increasing the P content of plant tissues, but is not capable of
379 increasing plant growth (Vázquez-de-Aldana et al. 2013). In the case of a more industrial
380 crop such as oil palm, it has been similarly found that filamentous fungus *Talaromyces*
381 *pinophilus* is capable of increasing P uptake and improving plant growth (Sembiring &
382 Wahyuni, 2018).

383 *Colletotrichum tofieldiae* is an endophytic fungus of *A. thaliana* that has been widely studied
384 as a promoter of plant growth through an increase in the plant content of P in deficiency
385 situations (Hiruma et al. 2016). Its application in crops such as tomato or maize has reported
386 a significant promotion of plant growth and yield, although it cannot yet be confirmed that
387 the same mechanisms described in *A. thaliana* are involved (Díaz-González et al., 2020).

388 **Iron acquisition**

389 Iron is a transition metal that is naturally present in two valences: Fe²⁺ (soluble) and Fe³⁺
390 (almost insoluble). Iron is required in several metabolic processes in plants, including the
391 tricarboxylic acid cycle, electron transport chain, oxidative phosphorylation, and
392 photosynthesis. It also regulates the biosynthesis of porphyrins, vitamins, antibiotics, toxins,
393 cytochromes, pigments, and aromatic compounds, and nucleic acid synthesis. In calcareous
394 soils, the concentration of dissolved ferrous iron is around 10⁻¹⁰ to 10⁻⁹ M, about two to three
395 orders of magnitude less than the concentration required by living organisms (10⁻⁷–10⁻⁵ M).
396 These environmental restrictions and biological requirements have resulted in the evolution
397 of a siderophore-mediated iron uptake system performed by some microorganisms.
398 Siderophores aid in transporting the originally insoluble ferric iron from the environment into
399 the cell (Saha et al. 2016; Rezanka et al. 2019).

400 In addition to the ability of different microorganisms to antagonize plant pathogens thanks to
401 the production of siderophores, which implies that bioavailability of iron for pathogens is

402 reduced, siderophores are capable of directly promoting plant growth. Although most of the
403 soil is blessed with sufficient iron for plant growth, plant iron deficiency is a common
404 problem in some ranges of soils, especially calcareous soil (30% of the world's agricultural
405 land), which may be due to the low solubility of Fe^{3+} hydroxide. The use of microbial
406 siderophores has been extensively studied and it was found that this organic molecule has
407 rescued plants from iron chlorosis. A significant improvement in some growth attributes and
408 plant health has been extensively observed after the treatment of seeds with siderophorogenic
409 bioinoculants. Siderophores play a crucial role in the dissolution of iron, hence making it
410 available for microbial and plant growth (Ansari et al. 2017).

411 The production of siderophores in plant endophytic fungi has been verified *in vitro* in several
412 crops, such as *P. vera* with species of filamentous fungi (*E. nigrum*, *Quambalaria*
413 *cyanescens*, *Trichoderma atroviride* or *T. harzianum*) (Dolatabad et al. 2017). In *Vigna*
414 *radiata*, the endophytic presence of yeast *Geotrichum candidum* leads to the promotion of
415 plant germination and growth, thanks to the production of siderophores, and also to this
416 ability to antagonize pathogenic bacteria *Xanthomonas campestris* (George et al. 2019).

417 An example of molecular characterization of siderophores produced by endophytic fungi can
418 be found in the so-called epichloënin A, which is unusual among ferrichrome siderophores
419 produced by the filamentous fungus *E. festucae* in interaction with *L. perenne* (Koulman et
420 al. 2012). In wheat, production of siderophores by filamentous endophytic fungi such as *A.*
421 *niger*, *T. aureoviride* and *T. harzianum* promotes plant growth (Ripa et al. 2019), as it has
422 been observed in *Phaseolus vulgaris* by *Trichoderma* sp., hence increasing root and aerial
423 parts length (Hoyos-Carvajal et al. 2009); it has been observed in cucumber by *T. asperellum*,
424 significantly promoting seedlings growth (Qi & Zhao, 2013), and in *C. chinense* by *B.*
425 *brongniartii*, increasing the fruit diameter (Toscano-Verduzco et al. 2020).

426 **Other nutrients acquisition**

427 Potassium (K) is, together with nitrogen and phosphorus, an essential element for plant
428 nutrition, being the third element in the classical chemical fertilizers NPK. Plants take this
429 element from the soil, but the high amounts of K present in soils correspond to insoluble
430 forms from rocks and silicate minerals. K deficiency affects the crop nutritional quality,

431 mechanical stability, and also pathogen resistance. In this sense, the solubilization of K by
432 microorganisms is a reliable alternative to make this element available for plants (Jaiswal et
433 al. 2016; Velázquez et al. 2016). Different fungi isolated from agricultural crops are capable
434 of solubilizing K *in vitro*. This is the case of endophytic filamentous fungi of tea *A. niger* and
435 *Penicillium sclerotiorum* (Nath et al. 2015).

436 Zinc (Zn) deficiency is the most common one and significantly affects crop production. Zn
437 is available in soils in the inorganic form, which is commonly not an available form for plant
438 assimilation. Zn-solubilizing microbes have been discovered in the soils of many crops and
439 tested as plant growth promoting factors (Kumawat et al. 2019). *P. sclerotiorum* is capable
440 of solubilizing Zn (Nath et al. 2015), which causes an increase in the plant nutrient
441 acquisition, as it has been verified with the presence of *S. indica* in lettuce, which has
442 increased the Zn concentration in their tissues, chlorophyll content and plant growth (Padash
443 et al. 2016). However, the greater acquisition capacity of Zn in *F. rubra* thanks to endophyte
444 *E. festucae* increases the nutrient content in plant tissues, but it does not increase its growth,
445 as it does the greater acquisition of Ca and Mg (Vázquez -de-Aldana et al. 2013). In contrast,
446 in *F. arundinacea*, fungus *Neotyphodium coenophialum* is capable of both increasing plant
447 acquisition of K, Ca and Mg, and increasing plant growth (Rahman & Saiga et al. 2005).

448 **Plant growth hormones production**

449 Plant hormones are the regulators of almost all aspects of plant development and plant
450 responses to the environment. Indole acetic acid (IAA) is the most common natural auxin
451 and has a positive effect on root growth. IAA affects plant cell division, extension, and
452 differentiation, stimulates seed and tuber germination, increases the rate of xylem and root
453 development, and initiates lateral and adventitious root formation, among many other
454 functions (Kumar et al. 2016). On the other hand, gibberellins (GAs) are a class of tetracyclic
455 diterpenoid hormones and have a key role in plant growth (Martínez et al. 2018). The ability
456 of different beneficial microorganisms to produce these compounds is an important
457 cornerstone in the development of sustainable agricultural systems.

458 Indol acetic acid (IAA)

459 Numerous endophytic yeast species have been found to have the ability to produce IAA *in*
460 *vitro*. From maize, species *Williopsis saturnus* has been isolated, being the first yeast
461 described with the capacity to produce IAA (Nassar et al. 2005). This capacity has also been
462 described later in other species, such as *Rhodospiridiobolus fluvialis* (Bunsangiam et al.
463 2019), or *Trichosporon asahii*, also isolated from sugarcane (Scarcella et al. 2017).
464 *Rhodospiridiobolus paludigenum* and *Cryptococcus flavus* species capable of producing
465 IAA *in vitro* have been isolated from rice leaves (Nutaratat et al. 2016); and the species
466 *Hanseniaspora opuntiae* and *Meyerozyma guilliermondii* from tangerine peel (*Citrus*
467 *reticulata*) (Ling et al. 2009). *Rhodospiridiobolus graminis* and *R. mucilaginoso* are the first
468 endophytic yeast strains isolated from *Populus* species (Xin et al. 2009), being able to
469 increase plant growth and fruit yields in squash plants, pepper and tomato, thanks to their
470 ability to produce IAA (Khan et al. 2012a). This is the same plant growth promotion observed
471 in *V. radiata* by *Geotrichum candidum* isolated from *Bruguiera cylindrica* (George et al.
472 2019) and by *C. tropicalis* in rice plants (Amprayn et al. 2012).

473 The *in vitro* ability of endophytic filamentous fungi to produce IAA has also been described
474 in non-agricultural plants, such as fungus *E. nigrum* from succulent *Caralluma acutangula*
475 (Ali et al. 2019), *Mucoromycotina guilliermondii* from pteridophyte *Drynaria quercifolia*
476 (Aban et al. 2017), and *Preussia* sp. from frankincense tree (Khan et al. 2016), hence
477 improving plant growth parameters. Also from crops, such as fungus *Aspergillus japonicus*
478 from *Euphorbia indica* (Hamayun et al. 2018), *A. niger* and *P. sclerotiorum* from tea (Nath
479 et al. 2015), *Colletotrichum fructicola* from *Coffea arabica* (Numponsak et al. 2018), *P.*
480 *variotii* from *C. acutangula* (Ali et al. 2019). and *Colletotrichum siamense* from leaves of
481 *Piper nigrum*, isolate that also exhibits antifungal capacity against common plant pathogenic
482 fungus *Cladosporium cladosporioides* (Munasinghe et al. 2017).

483 This IAA production capacity plays an important role in PGP in agricultural crops. In cereals,
484 this capacity has been related to increased growth in wheat plants, thanks to fungi *T.*
485 *harzianum*, *T. aureoviride* (Ripa et al. 2019), *Penicillium roqueforti* (Ikram et al. 2018), and
486 *Alternaria alternata*, isolated from *Elymus dahuricus* seeds and which also increases the
487 photosynthetic capacity and accumulation of nutrients in plant tissues (Quiang et al. 2019).

488 In rice, *Preussia* sp. and *A. niger* were able to promote plant growth (Al-Hosni et al. 2018;
489 Lubna et al. 2018); and *A. alternata* and *F. triticum* increased the chlorophyll content and the
490 length of the stem and root (Khan et al. 2015). *Penicillium* sp. and *Phoma glomerata* isolated
491 from cucumber are capable of increasing nutrient assimilation in rice by IAA production
492 (Waqas et al. 2012). In maize, the PGP capacity for IAA production has been reported in
493 species such as *P. chrysogenum*, *P. crustosum* (Hassan et al. 2017), *Bipolaris* sp. (Asaf et al.
494 2019), *F. oxysporum* (Mehmood et al. 2018a, 2018b) and *Aspergillus awamori* (Mehmood
495 et al. 2019). Also in vegetable crops like tomato, where *A. terreus* isolated from paprika
496 plants is able to produce IAA increasing plant growth, as well as suppressing the bacterial
497 speck disease caused by *Pseudomonas syringae* pathovar (pv.) tomato, *Colletotrichum*
498 *acutatum* and *R. solanacearum* (Yoo et al. 2018); *Capsicum chinense*, where *B. brongniartii*
499 isolated from *Carica papaya* increases the diameter of its fruits (Toscano-Verduzco et al.
500 2020); or cucumber, where *Paecilomyces formosus*, *T. asperellum* and *T. harzianum*
501 increases shoot length and allied growth (Khan et al. 2012b), seedling growth (Qi & Zhao,
502 2013) and plant biomass in soil and hydroponic experiments (Zhang et al. 2013),
503 respectively. Like it happens in other crops such as *Phaseolus vulgaris*, where *Trichoderma*
504 sp. increases the root and aerial parts length, thanks to the production of IAA (Hoyos-
505 Carvajal et al. 2009), or in *Mentha piperita* and *Thymus vulgaris*, where *S. indica* and
506 *Sebacina vermifera* increase the length and weight of roots and stems (Dolatabadi et al.
507 2012).

508 Gibberellins (GAs)

509 The ability of different species of endophytic filamentous fungi to produce GA *in vitro*, such
510 as *F. oxysporum* and *P. chrysogenum* isolated from tea (Nath et al. 2015), has been
511 determined. In cereals such as rice, GA production by various endophytic fungal species has
512 been determined to promote plant growth, such as *Aspergillus clavatus* (You et al. 2015),
513 *Gliomastix murorum* (Khan et al. 2009), *Penicillium citrinum* (Khan et al. 2008), *Phoma*
514 *glomerata* (Waqas et al. 2012) or *A. niger* (Lubna et al. 2018), isolated from *Nymphoides*
515 *peltata*, *Elymus mollis*, *Ixeris repenes*, cucumber and *Cannabis sativa*, respectively, which
516 are fungi capable of producing GA₁, GA₃, GA₄ and GA₇ and increasing the nutrient
517 assimilation capacity of the plant. It has been verified in the same way in maize plants by A.

518 *niger* (Lubna et al. 2018) or *Bipolaris* sp. isolated from *C. sativa* (Asaf et al. 2019). The same
519 ability to produce GA was reported in grasses, such as *Echinochloa crusgalli*, where
520 *Penicillium* sp. and *Aspergillus* sp. isolated from *Monochoria vaginalis* increase plant height
521 thanks to GA₃, GA₄ and GA₇ production (Ahmad et al. 2010).

522 Results were also reported in soybean by fungi *Cladosporium sphaerospermum*, *Phoma*
523 *herbarum*, *S. tshawytschae* and *Porostereum spadiceum*, which are capable of producing
524 GA₁, GA₃, GA₄ and GA₇ (Hamayun et al. 2009a, 2009b, 2009c, 2017); and in sunflower,
525 with an increase in vegetative biomass and photosynthetic activity by fungi *A. terreus* and
526 *Penicillium citrinum* (Waqas et al. 2015). We can also observe this in vegetables such as
527 tomato and cucumber, where *Penicillium janthinellum*, *Paecilomyces formosus* and
528 *Cladosporium* sp increase plant growth through GA₃, GA₄, GA₇ GA₁₂ and GA₁₉ production
529 (Hamayun et al. 2010; Khan et al. 2012b; Khan et al. 2013).

530 Other hormones

531 In the case of other hormones related to plant growth, nematophagous endophytic fungus
532 *Pochonia chlamydosporia* has been reported to be able to promote plant growth in barley by
533 inducing the production of brassinosteroids by plant tissues (Larriba et al. 2015).

534 **1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity**

535 ACC is the direct precursor of ethylene. Therefore, ACC deaminase activity acts by
536 degrading ACC, generating α -ketobutyrate and ammonia and thereby decreasing the
537 production of plant growth-inhibitory ethylene. ACC deaminase helps plants reduce many of
538 the manifestations of abiotic stress, promotes growth (generally increasing the length of roots
539 and aerial structures) and facilitates their adaptation and survival (del Carmen Orozco-
540 Mosqueda, et al. 2020)

541 ACC deaminase activity has been described *in vitro* in different species of endophytic
542 filamentous fungi, such as the *Penicillium purpurogenum* and *P. variotii* species isolated
543 from *C. acutangula* (Ali et al. 2019), or the *M. guilliermondii* species isolated from *D.*
544 *quercifolia* (Aban et al. 2017), thus highlighting its potential use for agricultural crop growth
545 and production. In crops, the ACC deaminase activity of *T. asperellum* when colonizing

546 cucumber roots has been compounded as significantly promoting the growth of seedlings (Qi
547 & Zhao, 2013). Similarly, endophytic yeast *Candida tropicalis* is capable of promoting rice
548 plant growth (Amprayn et al. 2012), and *G. candidum* isolated from *Bruguiera cylindrica* is
549 able to increase the germination rate and plant growth of *V. radiata* (George et al. 2019).

550 **Water acquisition**

551 The ability of different endophytic filamentous fungi to increase the availability of water in
552 the plant has been reported in several different crops. In grasses, such as *Festuca arundinacea*
553 and *Lolium arundinaceum*, fungus *Epichloë coenophiala* is probably able to increase water
554 availability thanks to affecting the soil water release path (Hosseini et al. 2016).
555 *Neotyphodium* spp. in *Lolium perenne* was able to increase water availability by root growth
556 promotion (Hesse et al. 2005). *L. multiflorum* seeds-colonization by *Neotyphodium* sp.
557 reduces germination when water is limiting, reducing the risk of seedling death (Gundel et
558 al. 2006). Furthermore, in *Brachiaria* spp. inoculated with *Sarocladium implicatum* were
559 reported the maintenance of plant water status and the increase in dry matter content, total
560 nonstructural carbohydrate contents and biomass (Odokonyero et al. 2016). In *Chenopodium*
561 *quinoa*, endophyte *S. indica* improves the water balance in the plant, thus increasing its
562 growth (Hussin et al. 2017), and in lettuce, the increase in the availability of water in plant
563 tissues by the action of *Trichoderma koningii* increases plant yield (Saia et al. 2019).

564 **CONCLUSIONS**

565 In the coming years, agriculture has to increase its productive capacity to feed a constantly
566 growing population. To achieve this, different strategies must be developed and adopted that
567 reduce damage to the environment and eliminate the dangers to our health, by reducing the
568 use of agricultural chemicals and increasing the use of beneficial microorganisms for plants.
569 In this scenario, endophytic fungi have great potential for use in agriculture.

570 In recent years, the development of new molecular and bioinformatics techniques has allowed
571 the identification of endophytic fungal species with the capacity to promote their host plant
572 growth, thanks to a wide variety of different mechanisms. Studies on microbial diversity in
573 new plant species and in different geographical situations and conditions will allow the

574 isolation of new endophytic fungal species with great potential for use in agriculture.
575 However, once the endophytic fungus has been identified with an interesting biological
576 activity in agriculture, it is essential to develop industrial scales that allow obtaining
577 profitable and safe inocula for their massive use in agricultural systems.

578 Finally, we must highlight the key importance that endophytic fungi have in the nutrient
579 cycle, which is vital in the development of sustainable agriculture. When the plant dies, the
580 endophytic fungi present in its tissues modify their way of life to saprophytic
581 microorganisms, decomposing the tissues that housed them and facilitating the addition of
582 nutrients to the soil. Moreover, endophytic phyllosphere fungi may affect plant litter quality,
583 organisms that control litter decomposition and the availability of nutrients in plant
584 communities.

585 Therefore, biofertilizer formulations can be made from endophytic fungi, reducing the use of
586 mineral fertilizers (with more research). In this sense, it is noteworthy that there is still a
587 small number of studies carried out in real agrosystems, something that is totally necessary
588 for their effective and efficient use in the agricultural market. Due to this, specific use
589 protocols and bioformulations can be developed, taking into account the soil and climate
590 characteristics, or the indigenous microbial communities.

591

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Table 1: Endophytic filamentous fungi and yeasts with PGP capacity.

Endophytic fungi	Species	Plant of origin	Crop of use	Mechanisms	References
Filamentous	<i>Acrocalymma</i> sp.	<i>Brassica oleracea</i> var. <i>acephala</i>	<i>B. oleracea</i> var. <i>acephala</i>	Not indicated	Poveda et al., 2020b
	<i>Alternaria alternata</i>	<i>Solanum nigrum</i>	Rice	IAA production	Khan et al. 2015
		<i>Elymus dahuricus</i>	Wheat	IAA production	Quiang et al. 2019
	<i>Aspergillus awamori</i>	<i>Withenia somnifera</i>	Maize	IAA production	Mehmood et al. 2019
	<i>A. brasiliensis</i>	Not indicated	Maize	P solubilization	Baron et al. 2018
	<i>A. clavatus</i>	<i>Nymphoides peltata</i>	Rice	GA production	You et al. 2015
	<i>A. japonicus</i>	<i>Euphorbia indica</i>	(<i>in vitro</i>)	IAA production	Hamayun et al. 2018
	<i>A. niger</i>	Tea (<i>Camellia sinensis</i>)	(<i>in vitro</i>)	IAA production K solubilizer	Nath et al. 2015
		Wheat	Wheat	Siderophores production N transfer	Ripa et al. 2019
		<i>Cannabis sativa</i>	Rice Maize	IAA production GA production	Lubna et al. 2018
	<i>A. sydowii</i>	Not indicated	Maize	P solubilization	Baron et al. 2018
	<i>A. terreus</i>	Paprika plants	Tomato	IAA production	Yoo et al. 2018
		Not indicated	Sunflower	GA production	Waqas et al. 2015
	<i>Aspergillus</i> sp.	<i>Monochoria vaginalis</i>	<i>Echinochloa crusgalli</i>	GA production	Ahmad et al. 2010

	<i>Byssochlamys nivea</i>	<i>Pistacia vera</i>	(<i>in vitro</i>)	P solubilization	Dolatabad et al. 2017
	<i>Beauveria bassiana</i>	Not indicated	<i>Phaseolus vulgaris</i>	Not indicated	Afandhi et al. 2019
	<i>B. brongniartii</i>	<i>Carica papaya</i>	<i>Capsicum chinense</i>	P solubilization IAA production Siderophores production	Toscano-Verduzco et al. 2020
	<i>Bipolaris</i> sp.	<i>Cannabis sativa</i>	Maize	IAA production GA production	Asaf et al. 2019
	<i>Cladosporium sphaerospermum</i>	Soybean	Soybean	GA production	Hamayun et al. 2009a
	<i>Cladosporium</i> sp.	Cucumber	Cucumber	GA production	Hamayun et al. 2010
	<i>Cochliobolus</i> sp.	Wheat	(<i>in vitro</i>)	P solubilization	Spagnoletti et al. 2017
	<i>Colletotrichum fruticicola</i>	<i>Coffea arabica</i>	(<i>in vitro</i>)	IAA production	Numponsak et al. 2018
	<i>C. siamense</i>	<i>Piper nigrum</i>	(<i>in vitro</i>)	IAA production	Munasinghe et al. 2017
	<i>C. tofieldiae</i>	Not indicated	Maize Tomato	Not indicated	Díaz-González et al., 2020
	<i>C. tropicale</i>	<i>Theobroma cacao</i>	<i>T. cacao</i>	N uptake	Christian et al. 2019
	<i>Curvularia</i> sp.	Wheat	(<i>in vitro</i>)	P solubilization	Spagnoletti et al. 2017
	<i>Curvularia</i> sp.	<i>B. oleracea</i> var. <i>acephala</i>	<i>B. oleracea</i> var. <i>acephala</i>	Not indicated	Poveda et al., 2020b
	<i>Diaporthe liquidambaris</i>	Rice	Rice	N uptake	Sun et al. 2019b

	<i>Drechslera sp.</i>	Wheat	(<i>in vitro</i>)	P solubilization	Spagnoletti et al. 2017
	<i>Epichloë coenophiala</i>	<i>Festuca arundinacea</i> <i>Lolium arundinaceum</i>	<i>F. arundinacea</i> <i>L. arundinaceum</i>	Water availability	Hosseini et al. 2016
	<i>E. festucae</i>	<i>Festuca rubra</i>	<i>F. rubra</i>	N acquisition P acquisition Zn acquisition Ca acquisition Mg acquisition Zn acquisition	Vázquez-de-Aldana et al. 2013
		<i>Festuca trachyphylla</i>	<i>Lolium perenne</i>	Siderophores production	Koulman et al. 2012
		<i>F. rubra</i>	<i>F. rubra</i>	P uptake	Zabalgogeoza et al. 2006
	<i>E. tembladerae</i>	<i>Bromus auleticus</i>	Carrot	Promotes symbiosis with arbuscular mycorrhizal fungi	Vignale et al. 2018
	<i>Epicoccum nigrum</i>	<i>Caralluma acutangula</i>	(<i>in vitro</i>)	IAA production Phosphates solubilization	Ali et al. 2019
		<i>P. vera</i>	(<i>in vitro</i>)	Siderophores production	Dolatabad et al. 2017
	<i>Fusarium sp.</i>	<i>B. oleracea var. acephala</i>	<i>B. oleracea var. acephala</i>	Not indicated	Poveda et al., 2020b
	<i>F. equiseti</i>	Turf grass	Cucumber	Not indicated	Saldajeno et al. 2011
		<i>Vicia villosa</i> and <i>Triticum aestivum</i>	Pea	Not indicated	Šišić et al. 2017
	<i>F. oxysporum</i>	Tea	(<i>in vitro</i>)	GA production	Nath et al. 2015

		<i>Wathenia somnifera</i>	Maize	IAA production N transfer	Mehmood et al. 2018a
		<i>Withania sominifera</i>	Maize	IAA production	Mehmood et al. 2018b
	<i>F. tricinctum</i>	<i>Solanum nigrum</i>	Rice	IAA production	Khan et al. 2015
	<i>Gaeumannomyces cylindrosporus</i>	(Pb-Zn mine tailings)	Maize	Photosynthetic rate increase	Yihui et al. 2017
	<i>Gliomastix murorum</i>	<i>Elymus mollis</i>	Rice	GA production	Khan et al. 2009
	<i>Heteroconium chaetospora</i>	<i>Brassica campestris</i>	<i>Brassica campestris</i>	N transfer	Usuki & Narisawa, 2007
	<i>Metarhizium brunneum</i>	Not indicated	Potato	N uptake P uptake	Krell et al. 2018a
		Not indicated	Potato	N uptake P uptake	Krell et al. 2018b
	<i>Mucoromycotina guilliermondii</i>	<i>Drynaria quercifolia</i>	(<i>in vitro</i>)	IAA production ACC deaminase activity P solubilization	Aban et al. 2017
	<i>Neotyphodium coenophialum</i>	<i>Festuca arundinacea</i>	<i>F. arundinacea</i>	P uptake K uptake Ca uptake Mg uptake	Rahman & Saiga et al. 2005
	<i>N. lolii</i>	Not indicated	<i>L. perenne</i>	P uptake	Ren et al. 2007
	<i>Neotyphodium</i> sp.	<i>Lolium multiflorum</i>	<i>L. multiflorum</i>	Not indicated	Vila-Aiub et al. 2005
		<i>L. multiflorum</i>	<i>L. multiflorum</i>	Water availability	Gundel et al. 2006
	<i>Neotyphodium</i> spp.	<i>Lolium perenne</i>	<i>L. perenne</i>	Water availability	Hesse et al. 2005

	<i>Ophiosphaerella sp.</i>	Wheat	(<i>in vitro</i>)	P solubilization	Spagnoletti et al. 2017
	<i>Paecilomyces formosus</i>	Cucumber	Cucumber	GA production IAA production	Khan et al. 2012b
	<i>P. variotii</i>	<i>C. acutangula</i>	(<i>in vitro</i>)	IAA production ACC deaminase activity P solubilization	Ali et al. 2019
	<i>Penicillium bilaiae</i>	Not indicated	Wheat Lentil	P solubilization	Wakwlin et al. 2007
	<i>P. citrinum</i>	Not indicated	Sunflower	GA production	Waqas et al. 2015
		<i>Ixeris repenes</i>	Rice	GA production	Khan et al. 2008
	<i>P. chrysogenum</i>	Tea	(<i>in vitro</i>)	GA production	Nath et al. 2015
		<i>Teucrium polium</i>	Maize	IAA production N transfer P solubilization	Hassan et al. 2017
	<i>P. crustosum</i>	<i>Teucrium polium</i>	Maize	IAA production N transfer P solubilization	Hassan et al. 2017
	<i>P. janthinellum</i>	Tomato	Tomato	GA production	Khan et al. 2013
	<i>P. purpurogenum</i>	<i>C. acutangula</i>	(<i>in vitro</i>)	ACC deaminase activity	Ali et al. 2019
	<i>P. radicum</i>	Not indicated	Wheat Lentil	P solubilization	Wakwlin et al. 2007
	<i>P. roqueforti</i>	<i>Solanum surattense</i>	Wheat	IAA production	Ikram et al. 2018
	<i>P. sclerotiorum</i>	Tea	(<i>in vitro</i>)	IAA production P solubilization K solubilizer	Nath et al. 2015

				Zn solubilizer.	
<i>Penicillium</i> sp.	<i>Monochoria vaginalis</i>	<i>Echinochloa crusgalli</i>		GA production	Ahmad et al. 2010
	Cucumber	Rice		IAA production GA production	Waqas et al. 2012
<i>Phialocephala fortinii</i>	Cypress, wild Japanese raspberry, skervish, wild strawberry, Japanese cedar, dandelion, phragmites, goldenrod, Japanese ginger and wheat	<i>Asparagus officinalis</i>		N uptake P transfer	Narisawa, 2017
<i>Phoma herbarum</i>	Soybean	Soybean		GA production	Hamayun et al. 2009c
<i>P. glomerata</i>	Cucumber	Rice		IAA production GA production	Waqas et al. 2012
<i>Phoma</i> sp.	<i>Tinospora cordifolia</i> and <i>Calotropis procera</i>	Maize		Not indicated	Kedar et al. 2014
<i>Phomopsis liquidambari</i>	<i>Bischofia polycarpa</i>	Peanut		N acquisition	Wu et al. 2019
	<i>B. polycarpa</i>	Rice		N uptake	Li et al. 2018
	<i>B. polycarpa</i>	Rice		N uptake	Yang et al. 2015
	Not indicated	Rice		N uptake	Sun et al. 2019a
	<i>B. polycarpa</i>	Rice		N uptake P uptake	Tang et al. 2019
	Rice	Rice		N uptake	Yang et al. 2014
<i>Pochonia chlamydosporia</i>	Not indicated	Tomato		Not indicated	Escudero et al. 2012

		Not indicated	Barley	Induction of brassinosteroids production	Larriba et al. 2015
	<i>Porostereum spadiceum</i>	Soybean	Soybean	GA production	Hamayun et al. 2017
	<i>Preussia sp.</i>	Frankincense tree	Rice	IAA production GA production	Al-Hosni et al. 2018
		Frankincense tree	(<i>in vitro</i>)	P solubilization IAA production	Khan et al. 2016
	<i>Pyrenophora sp.</i>	<i>B. oleracea var. acephala</i>	<i>B. oleracea var. acephala</i>	Not indicated	Poveda et al., 2020b
	<i>Quambalaria cyanescens</i>	<i>P. vera</i>	(<i>in vitro</i>)	Siderophores production	Dolatabad et al. 2017
	<i>Sarocladium implicatum</i>	<i>Brachiaria spp.</i>	<i>Brachiaria spp.</i>	Water availability	Odokonyero et al. 2016
	<i>Scolecobasidium humicola</i>	Tomato	Tomato	N uptake	Mahmoud & Narisawa, 2013
	<i>S. tshawytschae</i>	Soybean	Soybean	GA production	Hamayun et al. 2009b
	<i>Sebacina vermifera</i>	<i>Mentha piperita</i> <i>Thymus vulgaris</i>	<i>M. piperita</i> <i>T. vulgaris</i>	IAA production	Dolatabadi et al. 2012
	<i>Serendipita indica</i> (= <i>Piriformospora indica</i>)	<i>M. piperita</i> <i>T. vulgaris</i>	<i>M. piperita</i> <i>T. vulgaris</i>	IAA production	Dolatabadi et al. 2012
		Not indicated	Sweet basil	P acquisition	Sabra et al. 2018
		Not indicated	<i>Vigna mungo</i>	Not indicated	Kumar et al. 2012
		Not indicated	<i>Lactuca sativa</i>	Zinc acquisition	Padash et al. 2016

		Not indicated	<i>Chenopodium quinoa</i>	Improved water balance	Hussin et al. 2017
		<i>Galium album</i>	Wheat	P acquisition	Taghinasab et al. 2018
		Not indicated	Rapeseed	P solubilization	Wu et al. 2018
	<i>Setosphaeria rostrata</i>	Wheat	(<i>in vitro</i>)	P solubilization	Spagnoletti et al. 2017
	<i>Talaromyces pinophilus</i>	Not indicated	Oil palm	P uptake	Sembiring & Wahyuni, 2018
	<i>Trametes versicolor</i>	<i>G. album</i>	Wheat	P acquisition	Taghinasab et al. 2018
	<i>Trichoderma asperellum</i>	<i>Sorghum bicolor</i>	<i>S. bicolor</i>	Not indicated	Rajini et al. 2020
		Cucumber	Cucumber	P solubilization ACC deaminase activity IAA production Siderophore production	Qi & Zhao, 2013
	<i>T. aureoviride</i>	Wheat	Wheat	IAA Production Siderophores production	Ripa et al. 2019
	<i>T. atroviride</i>	<i>P. vera</i>	(<i>in vitro</i>)	Siderophores production	Dolatabad et al. 2017
	<i>T. gamsii</i>	Lentil	Maize Soybean Wheat Lentil	N transfer P solubilization	Rinu et al. 2014
	<i>T. koningii</i>	Not indicated	Lettuce	Water availability	Saia et al. 2019
	<i>T. harzianum</i>	Wheat	Wheat	IAA production Siderophores production N transfer	Ripa et al. 2019
		Not indicated	Cucumber	IAA production	Zhang et al. 2013

		<i>P. vera</i>	(<i>in vitro</i>)	Siderophores production	Dolatabad et al. 2017
	<i>Trichoderma</i> sp.	Not indicated	<i>Phaseolus vulgaris</i>	IAA production Siderophores production	Hoyos-Carvajal et al. 2009
	<i>Xylaria regalis</i>	<i>Thuja plicata</i>	Chilli	N uptake P uptake	Adnan et al. 2018
Yeast	<i>Candida valida</i>	Not indicated	Sugar beet	Not indicated	El-Tarabily, 2004
	<i>C. railenensis</i>	Maize	Maize	P uptake	Sarabia et al. 2018a
		Maize	Maize	P solubilization	Sarabia et al. 2018b
		Maize	Maize	P uptake	Sarabia et al. 2017
	<i>C. tropicalis</i>	Not indicated	Rice	IAA production ACC deaminase activity	Amprayn et al. 2012
	<i>Cryptococcus flavus</i>	Rice	(<i>in vitro</i>)	IAA production	Nutaratat et al. 2014
		Maize	Maize	P uptake	Sarabia et al. 2018a
		Maize	Maize	P uptake	Sarabia et al. 2017
	<i>Geotrichum candidum</i>	<i>Bruguiera cylindrica</i>	<i>Vigna radiata</i>	IAA production ACC deaminase activity Siderophores production	George et al. 2019
	<i>Hanseniaspora opuntiae</i>	<i>Citrus reticulata</i>	(<i>in vitro</i>)	IAA production	Ling et al. 2009
	<i>Meyerozyma guilliermondii</i>	<i>Citrus reticulata</i>	(<i>in vitro</i>)	IAA production	Ling et al. 2009
<i>Ficus religiosa</i>		Maize Chinese cabbage Lettuce	P solubilization	Nakayan et al. 2013	

		Maize	Maize	P solubilization	Sarabia et al. 2018b
	<i>Rhodosporidiobolus fluvialis</i>	Maize	(<i>in vitro</i>)	IAA production	Bunsangiam et al. 2019
	<i>Rhodotorula glutinis</i>	Not indicated	Sugar beet	Not indicated	El-Tarabily, 2004
	<i>R. graminis</i>	<i>Populus trichocarpa</i>	Squash plants Pepper	IAA production	Khan et al. 2012a
		<i>Populus sp.</i>	(<i>in vitro</i>)	IAA production	Xin et al. 2009
	<i>R. mucilaginosa</i>	<i>Populus sp.</i>	(<i>in vitro</i>)	IAA production	Xin et al. 2009
		<i>P. trichocarpa</i>	Tomato	IAA production	Khan et al. 2012a
		<i>Typha angustifolia</i>	Rice	N acquisition	Paul et al. 2020
	<i>R. paludigenum</i>	Rice	(<i>in vitro</i>)	IAA production	Nutaratat et al. 2016
	<i>Solicoccozyma aerea</i>	Maize	Maize	P solubilization	Sarabia et al. 2018b
	<i>Trichosporon asahii</i>	Not indicated	Sugar beet	Not indicated	El-Tarabily, 2004
		Sugarcane and maize	(<i>in vitro</i>)	IAA production	Scarcella et al. 2017
	<i>Williopsis saturnus</i>	Maize	(<i>in vitro</i>)	IAA production	Nassar et al. 2005