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1 **Ectomycorrhizal symbiosis helps plants to challenge salt stress conditions**

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30 **Abstract**

31 Soil salinity is an environmental constraint for plants that is currently increasing worldwide.
32 The most common salt ions within soils, sodium and chloride, are considered as beneficial for
33 plant development in small amounts, although their excess induces stress in most plants.
34 Sodium is usually considered the most toxic ion in the couple, mainly because it causes an
35 imbalance in the electrochemical gradients and competes with potassium for membrane
36 transport systems and binding sites within cells. In addition, the sudden exposition of plants to
37 salinity induces osmotic stress that imbalances root water and nutrient absorption and transport.
38 Within the different strategies that plants use to cope with salinity, their association with
39 beneficial soil microorganisms can play an important role in the adaptation to adverse
40 environments. Among them, ectomycorrhizal fungi, specialized in colonizing the roots of
41 woody plants, seem to have a protective effect on plants exposed to high amounts of salt.
42 Although no precise mechanisms for this enhanced plant salt tolerance have been described yet,
43 the improvement of plant water and mineral nutrition, and the restriction to sodium entrance
44 and extrusion of toxic ions from the photosynthetic organs are proposed as possible strategies.
45 This review aims at summarizing the current knowledge accumulated on the role of
46 ectomycorrhizal symbiosis in plant tolerance to salt stress.

47

48 **Keywords**

49 Ectomycorrhizal symbiosis, sodium, salt tolerance, trees, nutrient and water transport,
50 membrane transporters.

51

52 **Introduction**

53 Salinity, understood as the excess of sodium (Na^+) salts in the soil, is a detrimental condition
54 for plant performance that is increasing nowadays and challenges both agricultural crops and
55 natural ecosystems (Daliakopoulos et al. 2016). Salt stress induces both an osmotic and a toxic
56 effect in plants which disturbs major plant metabolic processes and hampers plant water and
57 nutrient balance. Exposure of plant roots to increasing NaCl will lead to competition of Na^+
58 ions with potassium (K^+) for its transporters so that Na^+ enters the plant cells through either
59 non-specific or selective transport systems (Wu 2018). Thus, Na^+ concentrations will build up
60 in the cytosol where it alters enzyme activity by displacement of the Ca^{2+} and K^+ ions of their
61 binding sites (Cramer et al. 1985; Rodríguez-Navarro 2000). The abundance of Na^+ ions also
62 changes the electrochemical gradient between both sides of the plasma membrane, affecting the
63 energization of soil nutrient uptake (Tavakkoli et al. 2010). Palliating these negative effects
64 diverts the energetic resources to detoxification, depleting other processes like nutrition, growth
65 or reproduction (Munns and Tester 2008).

66 Maintaining K^+ contents in the cell cytoplasm and its movements in the vascular tissues
67 is essential for salt-stressed plants to overcome the challenging environment (Shabala and Cuin
68 2008). Under salt stress, an initial massive influx of Na^+ in the root triggers a membrane
69 depolarization that provokes a K^+ efflux from the cytosol (Shabala et al. 2006), accompanied
70 by an increase in K^+ storage in the vacuole (Jiang et al. 2010). The drop in the cytosolic K^+
71 level induces high affinity transporters to boost the uptake from the roots (Shabala 2017). In
72 order to prevent Na^+ from reaching the photosynthetic organs, plants try to minimize its
73 accumulation in the tissues through changes in gene expression and protein function of
74 membrane transporters that aim at reducing the Na^+ uptake and at limiting its allocation to the
75 leaves, by extruding it out from root cells or into the vacuoles.

76 One of the first responses of plants to salinity will be the closure of stomata, the
77 reduction of transpiration, and the adjustment of the root water uptake. It is commonly accepted
78 that water is transferred from the soil to the root through two main paths, the cell wall continuum
79 (apoplastic path) and through the cell-to-cell path (symplastic path) which includes the transfer
80 of water through plasmodesmata and plasma membranes using specialized water channel
81 proteins called aquaporins. Aquaporins are membrane intrinsic proteins (MIPs) present in all
82 species, including fungi and plants (Nehls and Dietz 2014; Verdoucq and Maurel 2018). Under
83 different stresses including salinity, water uptake has been mainly attributed to the tight
84 regulation of aquaporins (Boursiac et al. 2005; Afzal et al. 2016). Plant cells also accumulate
85 compatible osmolytes or osmoprotectants. Although the role of compatible osmolytes has not

86 been fully unravelled, it has been observed that they protect against oxidative stress inside the
87 cells (Singh et al. 2015). Moreover, several studies have demonstrated that the overexpression
88 of genes leading to increased accumulation of these solutes can confer on plants the ability to
89 tolerate salinity (Parihar et al. 2015), and also, compatible solutes will alter how water is
90 uptaken by the roots (Aroca et al. 2012; Calvo-Polanco et al. 2014).

91 Taking all this into account, we observe that plants are not devoid of defence
92 mechanisms against salinity, at least in the short term. However, in the long run, these responses
93 may not be enough against a sustained stress and require further physiological, ecological and
94 evolutionary adaptations. This is the case of root symbioses, such as those established with
95 mycorrhizal fungi, in which the microorganism improves plant water uptake and mineral
96 nutrition. The extension of the exchange surface provided by the mycelium is an important
97 factor in the enhanced absorption of water and nutrients of mycorrhizal plants as the hyphae
98 are able to penetrate narrower pores (Bogeat-Triboulot et al. 2004; Lehto and Zwiazek 2011).
99 Another beneficial effect is the improvement of soil structure that facilitates plant rooting
100 (Rillig and Mummey 2006). All this translates in a stronger growth and higher biomass
101 accumulation in mycorrhizal plants, which have a better fitness and consequently adapt better
102 to challenging environments than in non-mycorrhizal conditions (Smith and Read 2008). So
103 far, most information on the beneficial effects of mycorrhizal plant-fungal interactions in plant
104 tolerance to salinity has been gathered from arbuscular mycorrhizal symbiosis revealing several
105 mechanisms involved (Evelin et al. 2009; Lenoir et al. 2016). Other symbioses, as the
106 ectomycorrhizal interactions specific to ligneous species, have evolved in many fungal and
107 plant lineages independently, contrarily to arbuscular mycorrhiza, which is considered a
108 plesiomorphy of plants (Field et al. 2015). This evolutionary diversity implies that the
109 association with ectomycorrhizal fungi can have multiple functional roles in the physiology of
110 the host. Little is known about ectomycorrhizal fungi concerning the mechanisms that
111 contribute to alleviation of the effects of salinity on their host plants. In this review we present
112 the research carried out thus far in this field and the main conclusions we can draw from them.

113

114 **Ectomycorrhizal fungi and the tolerance of plants to salt stress**

115 *Soil fungi differ greatly in their behaviour in saline environments*

116 The tolerance of fungi to salt stress has been often screened by measuring their capability to
117 adapt and grow in a culture medium supplemented with NaCl. Some extremophiles can grow
118 at saturating concentrations of NaCl in their natural environments (Gunde-Cimerman et al.
119 2009), whereas others are extremely sensitive. Regarding salt tolerance of ectomycorrhizal

120 fungal species, differences have been described between the two major phyla (Tresner and
121 Hayes 1971): as a general trend, Basidiomycota are less adapted to saline conditions than
122 Ascomycota, but some species are able to support relatively high NaCl concentrations (Zalar et
123 al. 2007). As a matter of fact, there are only 21 marine species of filamentous Basidiomycota,
124 very scarce compared to the 805 marine species of filamentous Ascomycota (Jones et al. 2015).
125 Overall, the salinity tolerance trait has been most studied in Basidiomycota. It is not necessarily
126 linked to specific clades but is found frequently in members of the same species or even the
127 same genus.

128 Ectomycorrhizal fungi are not usually found in environments of extreme salinity, such
129 as salt ponds, and it is unlikely that they play a role in hypersaline environments, since
130 halophytic plants are mostly herbaceous and non-mycorrhizal (Brundrett 2009, 2017),
131 However, they have been shown to be able to adapt to saline environments, and to adapt and
132 grow in a culture medium supplemented with NaCl by *in vitro* tests. These tests on salinity
133 tolerance of different fungal strains (Table 1) were achieved at NaCl concentrations of 120-800
134 mM of *e.g.* *Hebeloma* sp. or *Laccaria* sp. (Hutchison 1990; Kernaghan et al. 2002), and of
135 isolates of the same species as *Paxillus involutus* (Zhang et al. 2008), *Suillus* spp. (Hutchison
136 1990; Dixon et al. 1993; Bois et al. 2006a; Tang et al. 2009; Obase et al. 2010), and *Pisolithus*
137 *sp.* (Matsuda et al. 2006). In all cases, ion toxicity seems to be responsible for most of the
138 negative effects observed on fungal growth, compared to the osmotic component due to the
139 abundance of solutes in the environment (Dixon et al. 1993; Chen et al. 2001; Kernaghan et al.
140 2002; Bois et al. 2006a).

141 Also, some ectomycorrhizal fungi seem to have evolved towards salt tolerance and their
142 growth can even be stimulated by the application of moderate NaCl concentrations in the range
143 of 25-50 mM (Dixon 1993; Bois et al. 2006a; Matsuda et al. 2006) or higher (Zhang et al. 2008;
144 Obase et al. 2010). Recent studies using genomic techniques, have detected how populations
145 of the ectomycorrhizal fungus *Suillus brevipes* in North America are able to adapt to stress
146 associated with climate regimes and abiotic environments (Branco et al. 2015, 2017).

147
148 *Ectomycorrhizal fungi improve the tolerance of plants to salt stress with different strategies*
149 Thus far, few studies have shown improved plant salt stress tolerance by ectomycorrhizal fungi
150 compared to arbuscular mycorrhizal symbiosis. The effect of the presence of ectomycorrhizal
151 fungi in alleviation of stress symptoms seems to be fungus- and/or host-dependent. Dixon et al.
152 (1993) examined ectomycorrhizal *Pinus taeda* seedlings and found different responses
153 depending on the fungal inoculum. Whereas Na⁺ salts inhibited mycorrhization by some of the

154 fungal species tested, root colonization by *Pisolithus tinctorius* and *Laccaria laccata* was not
155 affected under 80 mM. Also, a positive effect on biomass accumulation was found at mild salt
156 stress (20-40 mM NaCl) on the seedlings mycorrhized with relatively salt-tolerant fungi. Other
157 studies have tried to look into further physiological details, particularly the nutritional status of
158 the plant to understand the specific processes for adaptation (see below). Complementarily to
159 mineral and water nutrition, other processes, such as the activation of stress response pathways
160 (metabolites, hormones) by ectomycorrhizal colonization can also play a role in the positive
161 effect against environmental stresses (Luo et al. 2009; Ma et al. 2014).

162 The mechanisms responsible for the enhancement of plant tolerance to salt stress by
163 ectomycorrhizal fungi are still unclear and several strategies could be involved. First, there is
164 an undeniable redistribution of Na⁺ ions in salt-stressed mycorrhizal plants compared to their
165 non-inoculated counterparts. It seems crucial for survival that Na⁺ does not reach the
166 photosynthetic tissues, and this protective effect has been found in seedlings inoculated with
167 salt-tolerant fungi. As a general rule, ectomycorrhizal seedlings subjected to salt stress were
168 able to load less Na⁺ to the shoots when inoculated with *Hebeloma spp.* (Muhsin and Zwiazek
169 2002a; Nguyen et al. 2006; Calvo-Polanco et al. 2008a, 2008b), *Laccaria bicolor* (Bois et al.
170 2006b; Nguyen et al. 2006; Calvo-Polanco et al. 2008b) and *Suillus tomentosus* (Calvo-Polanco
171 et al. 2008a). This effect could be linked to the strong extrusion Na⁺ by the fungus observed in
172 *Populus x canescens* - *P. involutus* symbioses (Li et al. 2012). In order to limit translocation of
173 toxic Na⁺ to the aerial parts, a successful strategy of plants is the storage of Na⁺ in the root
174 apoplasm, rather than in the vacuoles of root cells, avoiding its entrance into the symplastic
175 pathway (Ottow et al. 2005). It is very likely that the Na⁺ accumulated in the root tissues is
176 retained by the fungus, in order to protect the photosynthetic apparatus of the plant to keep its
177 production of carbon compounds.

178 These findings indicate that some ectomycorrhizal fungi function as a sort of “buffer”
179 or physical barrier between the external medium and the root in order to avoid the transfer of
180 toxic Na⁺ ions into the root cortex. Following this idea, Langenfeld-Heysler et al. (2007)
181 analysed *P. x canescens* inoculated with *P. involutus* and found that the fungus did not change
182 the Na⁺ and chloride (Cl⁻) contents in the root cell walls, particularly in those of the xylem
183 vessels, but somehow the fungus delayed the transfer of Na⁺ to the shoot. An intermediate result
184 was obtained by Ma et al. (2014) with two strains of *P. involutus*, one symbiotic and one non-
185 symbiotic. The inoculation of *P. x canescens* with each of the *P. involutus* lines impaired Na⁺
186 translocation to the shoot, even though one of the lines does not form functional mycorrhizae.
187 Although these results seem somehow contradictory, these studies have been done with

188 different ectomycorrhizal fungi on distant plant species, gymnosperms and angiosperms, that
189 do not necessarily have the same root and mycorrhizal structure and therefore it is expected that
190 the mechanisms of salt storage and transfer may differ.

191

192 *Ectomycorrhizal fungi improve plant mineral nutrition to alleviate salt stress*

193 The exclusion of Na⁺ from sensitive tissues is commonly accepted to be tightly related to K⁺
194 contents. Both ions are physico-chemically similar (Benito et al. 2014) and can be transported
195 partly by the same membrane proteins, but their roles and effects in plant cells are completely
196 different. Potassium is an essential macronutrient for plants, in which it is kept at high
197 concentrations (100-200 mM) to play many cellular and physiological roles, from membrane
198 energization to photosynthesis (Ahmad and Maathuis 2014; Dreyer et al. 2017). On the other
199 hand, Na⁺ is only beneficial in small amounts (in the nano- or micromolar range) and its excess
200 is harmful for plant tissues, except in some particular cases (Hasegawa et al. 2000). In salt stress
201 conditions, plants can suffer from K⁺ deficiency due to the competition with Na⁺ for uptake
202 systems at the plasma membrane (Botella et al. 1997). It has been demonstrated that
203 ectomycorrhizal fungi contribute to K⁺ nutrition of plants (Jentschke et al. 2001) especially
204 under conditions of K⁺ starvation (Garcia et al. 2014). Some species are able to improve the K⁺
205 content in the leaves of their host, especially in unfavourable conditions. This has been observed
206 in the symbiotic models *P. involutus* – *P. x canescens* (Langenfeld-Heyser et al. 2007; Luo et
207 al. 2009), *Scleroderma bermudense* – *Coccoloba uvifera* (Bandou et al. 2006) and *Hebeloma*
208 *crustuliniforme* – *Picea glauca* (Muhsin and Zwiazek 2002a). Li et al. (2012) demonstrated by
209 flux measurements that K⁺ homeostasis was maintained by *P. involutus* in salt stressed poplar,
210 thanks to the reduction of the salt-induced leakage of K⁺ and to the contribution of the fungus
211 to the host's absorption. Thus, an adequate K⁺ nutrition enhanced by the ectomycorrhizal
212 symbiosis seems to be crucial for a better adaptation of plants to environmental stresses, and in
213 particular to salinity (Munns and Tester 2008; Wang et al. 2013).

214 Another strategy against the detrimental effects of high levels of salts is given by the
215 advantageous effects of the presence of ectomycorrhizal fungi in the improvement of the
216 general mineral nutrition of the plant. Indeed, some ectomycorrhizal fungi are able to keep the
217 seedlings in a healthier state, for example by increasing the absorption of Ca²⁺, which is related
218 as well to the K⁺/Na⁺ ratio in the tissues (Ma et al. 2014), or by maintaining high phosphorus
219 and nitrogen contents in the seedlings (Muhsin and Zwiazek 2002a). Luo et al. (2011) also
220 found evidence that ectomycorrhizal poplar (*P. involutus*) conserved a better nutritional status,
221 which led to a reduced stress response and higher photosynthetic activity. A relative effect has

222 also been observed in plants that are adapted to saline environments, such as the tropical
223 seagrape *C. uvifera* (Bandou et al. 2006), whose ectomycorrhizal roots efficiently excluded Na^+
224 and Cl^- ions and enhanced the absorption of phosphorus. However, no changes in the
225 phosphorus content of salt-stressed mycorrhizal plants have been also reported (Langenfeld-
226 Heyser et al. 2007).

227

228 *Ectomycorrhizal fungi can regulate plant water transport under salt stress*

229 In addition to the effects of salinity in ion homeostasis, NaCl is a known inhibitor of aquaporin-
230 mediated water transport in roots (Boursiac et al. 2005; Lee et al. 2010) and is also related to
231 the reduction of plant transpiration. The inoculation of seedlings with ectomycorrhizal fungi
232 keeps them in an overall healthier transpiration rate (Muhsin and Zwiazek 2002b; Bois et al.
233 2006b; Calvo-Polanco et al. 2008b). Different studies in AM fungi (Barzana et al. 2015; Calvo-
234 Polanco et al. 2016) and ectomycorrhizal fungi (Marjanović et al. 2005; Hacquard et al. 2013;
235 Navarro-Ródenas et al. 2013; Xu et al. 2015; Peter et al. 2016) have already pointed out the
236 role of mycorrhizal fungi in modifying the expression and abundance of plant aquaporins under
237 different soil environmental conditions. The up-regulation of these traits has been usually linked
238 to an increase in the water transport capacity of plants (Xu et al. 2015), specially under stress
239 (Barzana et al. 2015; Calvo-Polanco et al. 2016). However, in some cases, ectomycorrhizal
240 symbiosis had no or even a negative effect on the root hydraulic conductivity (Calvo-Polanco
241 et al. 2011; Xu et al., 2016), but the specific processes responsible are still unknown. Taken
242 together, the role of fungal aquaporins as modulators of water transport in stress conditions
243 cannot be dismissed, as it might be one of the key factors for salt stress tolerance in combination
244 with activation of pathways that involves hormones and stress signal molecules and that will
245 need future studies.

246

247 **Membrane transport systems involved in symbiotic tolerance to salt stress**

248 Molecular mechanisms responsible for plant salinity tolerance mediated by ectomycorrhizal
249 symbiosis include membrane transport systems both at the fungal and at the plant root
250 membranes. Such membrane transporters would be critical for all the three adaptation strategies
251 shown by ectomycorrhizal symbioses, for Na^+ exclusion, K^+ nutrition and water transport (Fig.
252 1).

253 Regarding the barrier function of the fungus, it would be particularly interesting to
254 characterize the membrane transport systems responsible for Na^+ fluxes. The ENA1 ATPase
255 (Rodríguez-Navarro and Benito 2010) and the Na^+/H^+ antiporters Nha-like (Bañuelos et al.

256 1998; Proft and Struhl 2004), both involved in tolerance to NaCl in fungi, are promising
257 candidates for Na⁺ efflux from the fungus to the external medium. The first evidence for this
258 has been found in *S. brevipes* from a salinity area that had adapted to tolerate salt stress by
259 developing differential genomic regions including a gene encoding a membrane Na⁺/H⁺
260 antiporter (Branco et al. 2015). These results are also supported by experiments by Li et al.
261 (2012), in which the pharmacological inhibition of Na⁺/H⁺ antiporters of *P. involutus* had an
262 effect on its salt-induced extrusion of Na⁺. These results are also supported by experiments by
263 Li et al. (2012), in which the pharmacological inhibition of Na⁺/H⁺ antiporters of *P. involutus*
264 had an effect on its salt-induced extrusion of Na⁺. It is also possible that the excess of Na⁺ in
265 the fungus is stored in vacuoles or endosomes rather than in the cytosol, by members of the
266 VNX and NHX transporter families (Nass et al. 1997; Cagnac et al. 2007).

267 Potassium transporters and channels of the fungal and plant partners of the symbiosis
268 could cause a differential distribution of this ion within the mycorrhizal plant (Garcia and
269 Zimmermann, 2014). Selective fungal uptake transport systems, belonging to the Trk or HAK
270 families, could fight the excess of external Na⁺ with a higher selective absorption than plant
271 transporters. A further filter would be applied by the K⁺-selective channels that are thought to
272 release K⁺ into the plant apoplasm (Guerrero-Galán et al. 2018a, b). It is also likely that fungi
273 face the K⁺/Na⁺ imbalance through storage of K⁺ in the vacuole or Golgi and the Kha1
274 transporters could play this role. It is also noteworthy that, due to their similarity, Na⁺ and K⁺
275 can be permeated through the same transport systems with different affinities (Ariño et al.
276 2010).

277 In parallel to the K⁺ nutrition, fungal and plant aquaporins mediating water transport
278 (Fig. 1) and their regulation are involved in salt stress responses of ectomycorrhizal plants as
279 summarized above. These molecular players are well described in plants (Verdoucq and Maurel
280 2018) and have been identified in fungal genomes and partially characterized (Dietz et al. 2011;
281 Xu et al. 2015; Peter et al. 2016). For now, seven aquaporins have been found in the fungus *L.*
282 *bicolor*, of which *LbAQP1* is necessary for the development of functional ectomycorrhizae in
283 trembling aspen (Navarro-Ródenas et al. 2015). Interestingly, in transcriptomic analysis of the
284 symbiotic couple *Cenococcum geophilum-Pinus sylvestris* cultured under drought, one
285 aquaporin (Cenge3:604158) was up-regulated, suggesting that the fungus may help the plant to
286 cope with decreased water absorption or compensate the inhibition of plant aquaporins,
287 although no physiological differences with non-inoculation controls was reported (Peter et al.
288 2016). In the future, discoveries in the area of fungal genomics will open new horizons in the

289 study of plant-fungal symbiosis and are expected to be critical for the improvement of plant
290 adaptation to the presence of salt within the soil.

291

292 **The role of ectomycorrhizal associations in salt stress tolerance and their use for** 293 **reforestation**

294 In controlled *in vitro* or greenhouse experiments it is relatively easy to apply inocula and to
295 calculate the degree of root colonization. The fixed environmental conditions can be radically
296 different from those found in the real environment, where the climate and the existing
297 rhizospheric biodiversity can greatly change the result of the experiment (Weissenhorn et al.
298 2002; Onwuchekwa et al. 2014). It is possible that fungi selected and grown in laboratory
299 conditions are less competitive than the pre-existing microorganisms, and disappear from the
300 roots in a short time span (Onwuchekwa et al. 2014). In addition, although the effect of
301 ectomycorrhizae in growing seedlings is evident, it is still unknown to what extent
302 ectomycorrhizal fungi can improve salt tolerance of adult trees.

303 However, some research aimed to apply ectomycorrhizal symbiosis on plant seedlings
304 intended for ecological restoration of degraded areas, for example in the saline-alkaline soils
305 contaminated by composite tailing residues of bitumen extraction. In these areas, plants are
306 severely affected by accumulation of Na⁺, displaying reduced uptake of essential nutrients, such
307 as K⁺ and phosphorus, as well as leaf dieback (Renault et al. 1999). The first trials involved
308 direct testing of salts or composite tailing water on axenic cultures of ectomycorrhizal fungi to
309 assess which species and isolates were suitable for application in the field (Kernaghan et al.
310 2002; Bois et al. 2005). In parallel, several lots of autochthonous tree species were analyzed
311 (Khasa et al. 2002; Bois et al. 2006a,b; Nguyen et al. 2006; Yi et al. 2008; Calvo-Polanco et al.
312 2008b, 2011). The optimal combinations of plants and fungi have been tested in experiments
313 on oil sands reclamation sites with encouraging results with the prospect of a large-scale
314 application. Inoculated seedlings had higher survival rates and biomass accumulation than the
315 non-mycorrhizal plants, although the survival of the fungi in the root was not ensured
316 (Onwuchekwa et al. 2014; Hankin et al. 2015). Research efforts are still in progress to select
317 new pioneer symbiotic couples for land reforestation (Beaudoin-Nadeau et al. 2016).

318 To sum up, perspectives in this rather unexplored field of the use of ectomycorrhizal
319 associations to struggle with salt stress could range from molecular approaches to application
320 of ectomycorrhizal fungi in nurseries or forest cultures, offering exciting opportunities to
321 fundamental and applied research.

322

323

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607 **Legends of Figure & Table**

608

609 Figure 1. Fungal membrane transport systems are probably involved in plant protection against
610 salt stress through three different strategies. Three advantages of ectomycorrhizal symbiosis
611 seem to be involved in a better stress tolerance of plants and membrane transport systems
612 would play a role in all of them. First, Na⁺ exclusion from the plant would depend on the
613 extrusion of Na⁺ from the extraradical mycelium to the soil through ENA ATPases and Nha
614 transporters. The storage of the excess of Na⁺ within vacuoles by Vnx transporters could
615 also reduce the amount of Na⁺ that reaches the plant tissues. The second strategy is the
616 improvement of K⁺ nutrition by the fungus, thanks to Trk and HAK uptake transporters. This
617 ion would be transferred to the plant through TOK and/or SKC channels. Further uptake
618 through ACU ATPases or storage in vacuoles or vesicles through Nhx and Kha transporters
619 are also likely to occur. Finally, ectomycorrhizal fungi would help maintaining aquaporin-
620 mediated water transport, resulting in an improved water status of the symbiotic plant.

621

622 Table 1. Summary of the most studied salt-tolerant genera of ectomycorrhizal fungi: *Hebeloma*,
623 *Laccaria*, *Paxillus*, *Pisolithus*, *Rhizopogon* and *Suillus* (Basidiomycota). *means that the
624 studied isolate was not salt resistant.