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14 Abstract

Potassium (K⁺) is one of the most abundant elements of soil composition but its very low 15 availability limits plant growth and productivity of ecosystems. Because this cation 16 participates in many biological processes, its constitutive uptake from soil solution is crucial 17 for the plant cell machinery. Thus, the understanding of strategies responsible of K⁺ nutrition 18 19 is a major issue in plant science. Mycorrhizal associations occurring between roots and 20 hyphae of underground fungi improve hydro-mineral nutrition of the majority of terrestrial 21 plants. The contribution of this mutualistic symbiosis to the enhancement of plant K⁺ nutrition is not well understood and poorly studied so far. This mini-review examines the current 22 23 knowledge about the impact of both arbuscular mycorrhizal and ectomycorrhizal symbioses on the transfer of K⁺ from the soil to the plants. A model summarizing plant and fungal 24 transport systems identified and hypothetically involved in K⁺ transport is proposed. In 25 addition, some data related to benefits for plants provided by the improvement of K⁺ nutrition 26 27 thanks to mycorrhizal symbioses are presented.

Keywords: Potassium, Plant nutrition, Arbuscular mycorrhizal symbiosis, Ectomycorrhizal
symbiosis, Transport systems.

30

31 Introduction

32 Potassium (K^+) is one of the most important macronutrient for all organisms. In plants, K^+ 33 represents 2 to 10 % of the dry biomass, its optimal cytoplasmic concentration for enzyme activities being around 100-200 mM (Leigh and Wyn Jones, 1984). This cation participates to 34 35 various crucial processes such as plasma membrane polarization, growth, stomatal aperture or adaptation to environmental changes (Broadley and White, 2005; Wang and Wu, 2013; 36 37 Anschütz et al., 2014; Shabala and Pottosin, 2014). Maintaining an elevated K⁺ concentration in plant cells is vital for the smooth running of such physiological processes (Benito et al., 38 2014; Shin and Adams, 2014). Although K^+ ions are extremely abundant in soil, their 39 availability is very low due to their strong mineral adsorption. Depending on soil type, the K⁺ 40 41 concentration in soil solution is approximately 0.1 to 1 mM (Asher and Ozanne, 1967). This low availability combined to the constitutive demand of plants lead to the formation of 42 43 depletion areas around roots (Drew and Nye, 1969). Consequently, plants need to develop efficient strategies to improve the K⁺ uptake from soil (Zörb et al., 2013; Nieves-Cordones et 44 45 al., 2013), such as the acquisition of high-affinity transport systems or the establishment of plant-microbe associations. 46

47 Mycorrhizal symbioses are mutualistic interactions between the root systems of 48 around 80% of land plants and the mycelium of various fungi (Wang and Qiu, 2006). Among 49 mycorrhizal associations, two forms are mainly studied due to their ecological importance, 50 arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM). Mycorrhizal fungi participate 51 actively to plant development (Smith and Read, 2008) by improvement of access to nutrients, particularly when resources become scarce. In turn, vegetal partners provide up to 20-25% of 52 53 photosynthetic carbohydrates to their symbionts (Lopez et al., 2008). The improvement of plant nutrition through mycorrhizal symbioses and the molecular bases of nutrient transfer are 54 55 currently well studied for phosphorus (Javot et al., 2007; Plassard and Dell, 2010) and 56 nitrogen (Müller et al., 2007; Jin et al., 2012). However, only few data concern the possible mycorrhizal contribution to K⁺ acquisition (Benito and Gonzalez-Guerrero, 2014). 57

Herewith, we compiled and summarized the current knowledge concerning the role of AM and ECM symbioses in plant K^+ nutrition An overview of transport systems acting putatively in transfer of K^+ from soil to fungal cells and from fungi to plant cells is highlighted. Finally, improvement of K^+ acquisition by mycorrhizal associations will lead to benefits for the plant in diverse environmental conditions.

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65 Evidence of plant potassium nutrition by mycorrhizal symbiosis

66 Arbuscular mycorrhizal symbiosis

Plant K⁺ nutrition through the arbuscular mycorrhizal pathway has been rarely studied. 67 However, assessment of potassium distribution in AM fungi (*Rhizophagus irregularis*) using 68 69 particle-induced X-ray emission (PIXE) experiments (Johansson and Campbell, 1988) 70 revealed a strong K^+ accumulation in spores (Pallon et al., 2007), hyphae (Olsson et al., 71 2008), and vesicles (Olsson et al., 2011). Interestingly, PIXE analyses showed a higher K^+ 72 concentration in root-sections of Aster tripolium mycorrhized by R. irregularis than noninoculated plants, suggesting a possible increase of K⁺ acquisition due to the AM colonization 73 (Scheloske et al., 2004). Such a K⁺ enrichment of plants mycorrhized by various AM fungi 74 was also observed in Zea mays root steles (Kaldorf et al., 1999), in Pelargonium peltatum 75 76 shoots (Perner et al., 2007) and in *Lactuca sativa* leaves (Baslam et al., 2013). K⁺ transport 77 was commonly visualized by the utilization of rubidium (Rb^+) as an analog tracer. Measuring AM fungi mediated Rb^+ uptake from the soil, Hawkes and Casper (2002) showed putative 78 79 competition mechanisms for four herbaceous species.

80

81 Ectomycorrhizal symbiosis

Potassium fluxes from ECM fungi to host plants were first observed by determination of Rb⁺ 82 83 contents (Rygiewicz and Bledsoe, 1984; Jongbloed et al., 1991). Quantification of K⁺ in Picea abies cultivated in with 230 µM of K⁺ resulted in around 5-6 % of total K⁺ that came 84 85 from the ECM fungus Paxillus involutus (Jentschke et al., 2001). Regarding the cellular distribution of K⁺ within fungal hyphae, X-ray microanalysis showed localization mainly in 86 87 vacuoles of the ECM fungus Pisolithus tinctorius (Orlovich and Ashford, 1993; Ashford et al., 1999). PIXE experiments on P. sylvestris / Suillus luteus mycorrhizae revealed a high K⁺ 88 89 concentration in ectomycorrhizae vascular tissues (Turnau et al., 2001). Excitingly, data 90 obtained in multiple *Rhizopogon sp.* isolates from field showed an important K⁺ sequestration in rhizomorphs, that could be vital for forests subjected to long periods of K⁺ deprivation 91 92 (Wallander et al., 2002; Wallander and Pallon, 2005). Another fungus that can be considered as an important K⁺ accumulator is *Suillus granulatus* (Wallander et al., 2003). Strong mineral 93 degradation capacities of these two latter ECM fungi were suggested by the identification of 94 calcium-rich crystals originating from K⁺-rich mineral apatite on rhizomorph surfaces. Thus, 95 Rhizopogon sp. and S. granulatus could be considered as key facilitators between soil and 96 trees for K⁺ fluxes in temperate forest ecosystems. Recently, an increase of K⁺ contents of 97 98 about 35 % was observed in *Pinus pinaster* mycorrhized by *Hebeloma cylindrosporum* upon

99 2 months culturing in K⁺ deficiency, suggesting that this fungus plays a crucial role in pine 100 adaptation to limiting conditions (Garcia et al., 2014). K⁺ assimilation was improved also in 101 shoots of Acacia spirorbis and Eucalyptus globules mycorrhized by Pisolithus albus up to 102 38 % (Jourand et al., 2014). By contrast, Quercus ilex and Quercus faginea colonized by *Tuber melanosporum* displayed a significant reduction of K⁺ concentrations (Dominguez 103 104 Nunez et al., 2006). However, in another experiment, no difference in K^+ contents was 105 observed between control plants of Pinus halepensis, Q. faginea, and Quercus petraea, and 106 those inoculated with T. melanosporum (Dominguez Nunez et al., 2008). These contradictory data highlighted once again that K⁺ allocation from soil to plants through ECM fungi need 107 108 complementary functional investigations.

109

110 **Transport of potassium in mycorrhizal interactions**

111 Transport systems on the fungal side

112 Recent access to genomes of ECM fungi Laccaria bicolor (Martin et al., 2008), 113 T. melanosporum (Martin et al., 2010) and many others (http://genome.jgi.doe.gov/Mycorrhizal_fungi/Mycorrhizal_fungi.info.html) 114 allows the 115 identification of new candidate genes involved in mycorrhizal resource exchanges (Casieri et al., 2013). Consequently, four families of putative K⁺ transport systems could be identified in 116 117 ECM fungi (Figure 1) on the basis of their homology to yeast Trk transporters (Ko and Gaber, 1991), to yeast TOK channels (Ketchum et al., 1995), to bacterial and yeast KT/KUP/HAK 118 119 transporters (Bossemeyer et al., 1989, Bañuelos et al., 1995) and to animal Shaker-like 120 channels (SKC) (Papazian et al., 1987; Jan and Jan, 1997). Before availability of these 121 genomes, a Trk-type transporter and a *Shaker*-like channel were identified in an EST library 122 of H. cylindrosporum (Lambilliotte et al., 2004). The member of the Trk/Ktr/HKT family 123 (Corratgé-Faillie et al., 2010) was functionally characterized. *Hc*Trk1 was shown to restore 124 partially the wild-type phenotype of a yeast strain deficient in K^+ uptake (Corratgé et al., 2007). Moreover, electrophysiological analyses performed by expression of cRNA in 125 *Xenopus* oocytes argued that HcTrk1 might function as a Na⁺-K⁺ transporter. More recently, 126 127 the use of H. cylindrosporum transgenic lines allowed the localization of this transporter exclusively in external hyphae of P. pinaster mycorrhizae (Garcia et al., 2014), suggesting a 128 129 specialized reorganization of *Hc*Trk1 to uptake sites. The other candidate identified in the *H*. 130 cylindrosporum EST library belongs to the SKC family representing voltage-dependent K⁺selective channels (Lambilliotte et al., 2004). Interestingly, SKC channels were found 131 132 exclusively in Basidiomycota fungi and in some members of basal fungi, whereas they are

absent in sequenced *Ascomycota*, suggesting a loss of these K^+ channels in this clade. Excitingly, the *H. cylindrosporum* genome accession provides now two additional types of transport systems, three *Hc*TOK channels and a *Hc*HAK transporter. The analysis of these new candidates is currently in progress in order to dissect the whole K^+ transportome of *H. cylindrosporum*.

Transporters and channels of AM fungi are still the missing part of the K⁺ transport 138 from soil to host. Four sequences of R. irregularis from an EST library 139 (http://mycor.nancy.inra.fr/IMGC/GlomusGenome) were identified as K⁺ transport systems 140 (Casieri et al, 2013). Three of them are coding for SKC-type channels and one for a 141 142 KT/KUP/HAK transporter. Interestingly, no Trk and TOK members were identified from this 143 library, and even from the sequenced nuclear genome 144 (http://genome.jgi.doe.gov/Gloin1/Gloin1.home.html). Functional characterization and 145 analysis of these new candidates will provide more precise information on fungal molecular 146 players involved in AM plant K⁺ nutrition.

Future research on AM and ECM K⁺ transport systems need to precise their putative 147 involvement in K^+ uptake from the soil or in K^+ release towards plant cells. Based on 148 149 homology, it is tempting to argue that transporters of the Trk/Ktr/HKT and KT/KUP/HAK 150 families could take up K⁺ from the soil. Similarly, *Shaker*-like K⁺ and TOK channels could be 151 probably involved in the transfer of K⁺ from the arbuscule or Hartig net to host plant cortical 152 cells (Figure 2; Benito and Gonzalez-Guerrero, 2014). However, caution must be taken on 153 these predictions due to the possible bidirectional behavior of some transport systems in 154 specific conditions and due to their unknown subcellular localization.

155

156 Transport systems on the plant side

157 The direct pathway of woody plant K^+ uptake (Figure 2A) is poorly studied so far in contrast 158 to model plants as e.g. Arabidopsis thaliana (Alemán et al., 2011; Dreyer and Uozumi, 2011; Coskun et al., 2013; Nieves-Cordones et al., 2013). However, some K⁺ transport systems in 159 160 woody plants able to form ECM associations have been identified. For example, two channels 161 expressed in roots of Populus euphratica (PeKC1 and PeKC2) were characterized (Zhang et al., 2010). Interestingly, their over-expression led to complementation of the A. thaliana akt1 162 163 mutant. Because AKT1 is involved in K⁺ acquisition in A. thaliana (Hirsch et al., 1998), this finding strongly suggests that these two transport systems could play a role in K⁺ nutrition in 164 165 poplar trees. However, their role in context of mycorrhizal associations has not been 166 dissected. Their expression analysis upon AM and ECM symbioses would be a good starting

point for the identification of transport systems required in K^+ nutrition, as already shown for phosphate transporters of *Populus trichocarpa* (Loth-Pereda et al., 2011). In turn, in AM plants, the direct pathway of K^+ uptake is well known since many years (Figure 2B), several transport systems were identified, functionally characterized and their role in K^+ nutrition in various conditions was investigated. These proteins belong to the transporter families Trk/Ktr/HKT (Corratgé-Faillie et al., 2010) and KT/KUP/HAK (Grabov, 2007), as well to the *Shaker*-like channels (Dreyer and Uozumi, 2011).

Very few studies investigated so far the plant K⁺ transportome of the mycorrhizal 174 pathway (Figure 2C, D). Recently two ESTs of P. sylvestris representing the SKOR-type 175 176 outward Shaker-like channel were found to be highly up-regulated during ECM interaction 177 with Ceonococcum geophilum, and less up-regulated upon interaction with S. granulatus and 178 *Rhizopogon roseolus* (Martina Peter, pers. comm.). A KT/KUP/HAK transporter was found to 179 be 44-fold up-regulated in Lotus japonicus mycorrhized by the AM fungus Gigaspora 180 margarita (Guether et al., 2009). More recently, a SKOR channel of Z. mays was identified to 181 be up-regulated by AM colonization in response to salinity (Estrada et al., 2013). Future 182 analyses of these first plant candidates are needed to dissect the molecular bases of K⁺ uptake 183 from the plant-fungus interface.

184

185 Benefits of mycorrhizal potassium uptake for plants

186 Improvement of salt and drought stress tolerance

Advantages conferred by K⁺ originating from mycorrhizae include improved stress tolerance 187 188 of the host plant. Acquisition of plant salinity tolerance by AM symbiosis has been described 189 for several decades (Hirrel and Gerdemann, 1980; Ojala et al., 1983), very little is known 190 about physiological and molecular mechanisms enhancing this adaptation. AM colonization 191 enhances the plant K⁺ uptake whereas the Na⁺ content is maintained at low levels in salt stress conditions applied to Vicia faba (Rabie and Almadini, 2005), Acacia nilotica (Giri et al., 192 193 2007), Ocimum basilicum (Zuccarini and Okurowska, 2008), Glycine max (Sharifi et al., 2007), Olea europaea (Porras-Soriano et al., 2009) or Z. mays (Estrada et al., 2013). These 194 195 data indicate that AM symbiosis improves salt tolerance of the host plant through the modification of the K^+/Na^+ balance. This finding was corroborated by high internal K^+ 196 197 concentrations in several AM fungi collected in natural saline sites (Hammer et al., 2011a). 198 Recently, Estrada et al. (2013) demonstrated differential expression levels during AM 199 colonization for three K^+ transport systems of Z. mays putatively involved in phloem 200 loading/unloading (ZmAKT2), xylem release (ZmSKOR) and Na⁺/K⁺ homeostasis (ZmSOS1).

These exciting findings open the way to the elucidation of plant proteins involved in transport of K^+ originating from mycorrhizal fungi, especially under salt stress conditions.

203 Input of AM symbiosis on drought stress resistance of plants has been well studied 204 (Harley and Smith, 1983; Al-Karaki, 1998; Porcel and Ruiz-Lozano, 2004). Improvement in hydric stress tolerance is accompanied by an elevation of K^+ concentrations observed *e.g.* in 205 206 *Citrus tangerine* (Wu and Xia, 2006), indicating a role of AM symbiosis through K⁺ uptake required for osmotic adjustment. Interestingly, El-Mesbahi et al. (2012) demonstrated that 207 208 hydraulic conductivity of AM-colonized Z. mays growing under hydric stress was enhanced by supply of K^+ in external medium. Moreover, the expression level of the plant aquaporin 209 ZmPIP2;6 was modulated by K^+ supply in hydric stress, suggesting a tight link between 210 adaptation of mycorrhized plants to drought stress and K⁺ resource availability. 211

Salt and drought stress tolerance linked to potassium nutrition has been so far less studied in ECM plants. However, recently, Danielsen and Polle (2014) have been shown an increase of K^+ in ECM poplar under drought conditions suggesting also in this symbiotic interaction a role of mycorrhizal K^+ for environmental stress adaptation.

216

217 Interaction between plant potassium and phosphorus nutrition

Interestingly, a strong correlation between K⁺ and phosphorus (P) during AM symbiosis was 218 219 reported. Olsson and co-authors (2008, 2011) highlighted a co-distribution and a linked ratio of K⁺ and P in *R. irregularis* spores, hyphae and vesicles. When spores were enriched in P, an 220 221 increase of K⁺ content was observed (Olsson et al., 2011). Several studies on ECM symbiosis 222 reported similar results. Indeed, a strong correlation in K⁺ and P distribution was described in 223 rhizomorphs of Rhizopogon sp. using PIXE analyses (Wallander and Pallon, 2005). Other 224 studies showed that the decrease of P availability in soil could lead to either a decrease or an 225 increase of K⁺ content in ECM with *Pinus rigida* (Cumming, 1993) or in AM with *Trifolium* subterraneum (Smith et al., 1981), respectively. Moreover, K⁺ and P were found in same 226 fungal compartments of P. involutus such as vacuoles (Orlovich and Ashford, 1993; Ashford 227 et al., 1999). Interestingly, it is assumed that K^+ is one of the major counter-ions of 228 polyphosphate (polyP) granules, especially of soluble polyP short-chains mainly located in 229 230 fungal vacuoles (Bücking and Heyser, 1999). Recently, elemental analysis of spherical 231 electron-opaque granules in the vacuoles of *Scleroderma verrucosum* hyphae associated with Quercus acutissima using TEM-EDS (Transmission electron microscopy-energy-dispersive 232 Xray Spectroscopy) showed major correlated peaks for P and K (Jung and Tamai, 2013). In 233 addition, we have revealed recently that the over-expression of a K^+ transporter of H. 234

cylindrosporum led to an alteration of K⁺ and P translocation from roots to shoots of 235 236 mycorrhized *P. pinaster* under K⁺ deprivation (Garcia et al., 2014), providing new evidences for K^+ and P interaction during their transport in ECM symbiosis. All these data 237 238 demonstrating the strong link between these two elements suggest that K⁺ seems to be a more important component of mycorrhizal symbiosis than formerly suspected. Therefore, K⁺ needs 239 240 to be considered not only as a direct trophic element involved in plant K⁺ nutrition, but also as an "indirect-trophic" component required for homeostasis and correct transfer of other 241 242 nutrients to the host plant, such as inorganic phosphate. Moreover, Hammer et al. (2011b) described a K⁺ accumulation in an AM fungus related to low C supply from the plant. 243 244 Consequently, we can imagine that in conditions of low availability of C originating from the host plant, the high concentration of K⁺ observed in the fungus could be related to the 245 accumulation of P (in polyP form) which is not transferred to the plant. However, additional 246 247 investigations are needed to validate or not this hypothesis and to get more insight on the interaction occurring between K⁺, P and C in mycorrhizal symbioses. 248

249

250 Protection against radiocaesium pollution

Radiocaesium isotopes (¹³⁴Cs, ¹³⁷Cs) are important soil contaminants that can enter the food 251 252 chain by the intermediate of plant uptake (Delvaux et al., 2001). It is well known that external 253 K⁺ affects the acquisition of radiocaesium by plants (Tamponnet et al., 2008). Involvement of 254 mycorrhizal symbiosis on radiocaesium uptake was reported. Evaluation of the Cs^+/K^+ ratio in P. abies showed a lower acquisition of ¹³⁴Cs by plants inoculated with Hebeloma 255 *crustuliniforme* due to its retention in the outer hyphae and to a better transfer of K⁺ to the 256 plant (Brunner et al., 1996). By contrast, P. pinaster mycorrhized by R. roseolus displayed 257 more elevated concentrations in ¹³⁴Cs than non-mycorrhized plants, whereas the K⁺ content 258 259 remained stable (Ladeyn et al., 2008), highlighting the importance of the considered hostsymbiont couple. The influence of K^+ on ^{134}Cs accumulation was also investigated in AM 260 symbiosis, in Medicago truncatula colonized by R. irregularis radio. Caesium accumulation 261 of plants seems to be inversely correlated to K⁺ contents in the external medium (Gyuricza et 262 al., 2010a). Based on these results, AM symbiosis combined with high K⁺ concentrations in 263 external medium would be crucial to avoid ¹³⁴Cs accumulation in plants growing on 264 contaminated soil. Interestingly, external P elicits the same effects as K⁺ on ¹³⁴Cs uptake 265 during AM colonization of *M. truncatula* (Gyuricza et al., 2010b), reinforcing the idea of a 266 close relationship between K⁺ and P via polyP synthesis, storage and transport. In contrast to 267 these studies, pot experiments by Joner et al. (2004) with different external K⁺ concentrations, 268

three host plants and two AM fungal species indicated that AM effects on plant ¹³⁴Cs and ¹³⁷Cs accumulation could be negligible. Further investigations will be needed to conclude whether mycorrhizal associations play a direct, via transport processes, or an indirect role on plant protection to radiocaesium contaminated soils.

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274 Conclusion

Although the role of K^+ is still poorly investigated in mycorrhizal studies, it appears that plant K⁺ nutrition is clearly improved by mycorrhization, especially under K⁺ limiting conditions as *e.g.* found in forest ecosystems. Moreover, this improvement could act on abiotic stress tolerance, P homeostasis maintenance, or exclusion of soil contaminants such as radiocaesium. Thanks to genome and transcriptome access, the dissection of molecular mechanisms involved will be unraveled in the coming years, strengthening our knowledge on the mycorrhizal contribution to plant K⁺ nutrition.

282

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557 Figure 1: Phylogenetic trees of potassium transport systems from sequenced 558 mycorrhizal fungi.

Four families of K^{T} transport systems were identified in sequenced mycorrhizal fungi. Two of 559 560 them code for putative transporters, for the (A) Trk and (B) HAK families, and the two others 561 for putative ion channels, for the (C) TOK and (D) Shaker-like (SKC) families, respectively. 562 (A) Two sub-families of Trk transporters were identified in Basidiomycota. (C) Two 563 subfamilies of TOK channel were found in Asco- and Basidiomycota. Neither of these two 564 families were identified in the *Glomeromycota* species *Rhizophagus irregularis*. (D) No SKC channel was found in Ascomycota fungi (mycorrhizal or not), suggesting the loss of this 565 566 channel in this clade. Structure models of each family are represented. Transmembrane 567 domains are symbolized by rectangles and pore domains by a P. The voltage-dependent 568 domain of SKC proteins (D) is indicated by a red rectangle (+++). Trees were constructed

using maximum likelihood method with 100 bootstraps. Green, yellow and red circles 569 570 indicate successful published, successful unpublished (Zimmermann et al.) or failed unpublished functional characterization, respectively. Am: Amanita muscaria, Be: Boletus 571 572 eludis, Cgeo: Cenococcum geophilum, Cglau: Cortinarius glaucopus, Cv: Choiromvces 573 venosus, Hc: Hebeloma cylindrosporum, Gl: Gyrodon lividus, La: Laccaria amethystina, Lb: 574 Laccaria bicolor, Mb: Meliniomyces bicolor, Mc: Morchella conica, Mv: Meliniomyces variabilis, Om: Oidiodendron maius, Pc: Piloderma croceum, Pi: Paxillus involutus, Pm: 575 Pisolithus microcarpus, Pr. Paxillus rubicundulus, Pt. Pisolithus tinctorius, Ri: Rhizophagus 576 577 irregularis, Sb: Suillus brevipes, Sc: Scleroderma citrinum, Sl: Suillus luteus, Sv: Sebacina 578 vermifera, Tb: Terfezia boudieri, Tc: Tulasnella calospora, Tmat: Tricholoma matsutake, 579 Tmel: Tuber melanosporum, Wm: Wilcoxina mikolae. Lengths of aligned sequences are 580 around 1000, 800, 900 and 500 amino acids for Trk, KUP, TOK and SKC proteins, 581 respectively. Saccharomyces cerevisiae (SaccTrk1 and SaccTrk2 (A), SaccTOK (C)), Debaryomyces occidentalis (DoHAK1 (B)) and Xenopus laevis (XIKV2.1 (D)) protein 582 sequences were selected as outgroups to root trees. All sequences were picked up on the 583 mycorrhizal JGI 584 fungi genome portal: 585 http://genome.jgi.doe.gov/Mycorrhizal fungi/Mycorrhizal fungi.info.html.

586 Figure 2: Current knowledge about potassium transport systems in mycorrhizal 587 associations.

(A, B) The transfer of potassium (K^{+}) from the soil to plant cells by the direct pathway needs 588 plant transport systems in root uptake and release sites. (A) Shaker type channels from 589 Populus euphratica (PeKCs) and a KUP transporter of Populus trichocarpa (PtKUP) could 590 be involved in K⁺ uptake in poplar trees (Zhang et al., 2010). **(B)** Members of HKT, HAK and 591 Shaker families were identified and characterized in various AM plants as transport systems 592 involved in K nutrition. (C) To our knowledge, only K^{+} transport systems of the fungus 593 594 Hebeloma cylindrosporum are currently analyzed in ECM symbiosis, and just one, HcTrk1, is 595 already characterized (Corratgé et al., 2007; Garcia et al., 2013). Few transcriptomic data suggest the role of some plant proteins allowing K^+ uptake from the apoplasm. (D) EST 596 library of *Rhizophagus irregularis* allows the identification of several K⁺ transport related 597 598 proteins (Casieri et al., 2013), and transcriptomic analysis revealed an highly overexpression of a K⁺ transporter in inoculated Lotus japonicus (Guether et al., 2009). Full lines indicate 599 transport systems whose capability in K^{+} transport was verified. Dotted lines indicate 600

transport systems whose involvement in K^+ transport during mycorrhizal symbioses is suggested. ECM fungal structures: Extraradical hyphae (ERM), fungal mantle and Hartig net. AM fungal structures: ERM, spore, hyphopodium and arbuscule. Plant root cells: roots hair, epidermal cells and cortical cells, central cylinder. *Hc: Hebeloma cylindrosporum, Ri: Rhizophagus irregularis, Pe: Populus euphratica, Pt: Populus tremula, Ps: Pinus sylvestris, Lj: Lotus japonicus.*

Figure 1.TIF









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