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# New Phytologist

## Latitudinal constraints in responsiveness of plants to arbuscular mycorrhiza: The 'sun-worshipper' hypothesis.

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7 Latitudinal constraints in responsiveness of plants to arbuscular mycorrhiza: The  
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9

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27

28 **Keywords**

29 Arbuscular mycorrhiza; eco-evolutionary processes; environmental filtering;

30 Glomeromycotina; mycorrhizal responsiveness; phenotypic adaptation; plant biogeography;

31 the sun-worshipper hypothesis

32

33

34

35 Most terrestrial plants depend strongly on associations with arbuscular mycorrhizal (AM)  
36 fungi (Subphylum: Glomeromycotina) to establish and survive (Bever, 2002; van der Heijden  
37 *et al.*, 1998; Klironomos *et al.*, 2011; Veresoglou *et al.*, 2017), and have evolved a nutritional  
38 mutualism. In this mutualism, the plant provides carbon to the fungus, usually subject to the  
39 availability of light (Hayman 1970; Heinemeyer *et al.*, 2003; Shi *et al.* 2014; Konvalinkova &  
40 Jansa, 2016), and the fungus provides the plant with mineral nutrients acquired from soil.  
41 Because of light constraints, it is expected that latitude exerts a strong influence on reciprocal  
42 exchange of resources between mycorrhizal plants and fungi, and this could have  
43 consequences on the responsiveness of plants to mycorrhizal fungi. Latitude induces changes  
44 in the amount of solar energy and the timing when this is made available to primary producers  
45 during the year and in the day. At the same time, there is a strong negative relationship  
46 between latitude and temperature that may also impact the functioning of the mycorrhizal  
47 symbiosis, and in some cases (e.g. in north temperate systems), a general relationship between  
48 latitude and several edaphic factors (Read and Perez-Moreno 2003).

49 There is compelling evidence that the alpha-diversity of Glomeromycotan fungi,  
50 which form AM symbioses, decreases with latitude (Davison *et al.*, 2015). This finding can be  
51 partially explained by the transition from ecosystems dominated by AM host plants in the  
52 tropics, to ectomycorrhizal and ericoid mycorrhizal dominated ecosystems at higher latitudes  
53 (Smith & Read, 2008). We know less about the extent to which latitude impacts the  
54 functioning of AM symbioses, which could occur either through latitudinal differences in  
55 solar radiation or resulting changes in temperature (Clarke & Gaston, 2006; Schluter, 2016).  
56 Here, we propose the ‘sun-worshipper’ hypothesis that discriminates three different types of  
57 underlying responses of latitudinal gradient-induced changes in plant host mycorrhizal  
58 responsiveness (Fig. 1). Changes in abiotic conditions may allow plants to derive more  
59 benefits from the symbiosis at lower latitudes through phenotypic plasticity (mechanism one –  
60 Fig.1). A likely example of phenotypic plasticity might involve changes in the expression of  
61 genes that allow crosstalk with AM fungi when light availability is low as has been shown for  
62 drought (Li *et al.*, 2016). Abiotic conditions more favourable for the symbiosis close to the  
63 tropics could further exclude, via competition, species less dependent on AM fungi, resulting  
64 in distinct plant communities from a perspective of AM fungal-associating behaviour; such a  
65 process can be described as environmental filtering (mechanism two – Fig. 1). Finally, we  
66 know that AM plants at high latitudes encounter a less diverse pool of potential symbiotic  
67 partners (e.g. because of the observed latitudinal gradient in Glomeromycotan diversity;  
68 Davison *et al.*, 2015) and at the same time communities at high latitudes are in general

69 dominated by plants that associate with ectomycorrhizal and ericoid mycorrhizal fungi. Plants  
70 distant from the tropics could thus form less profitable AM symbioses (but also support fewer  
71 AM partners) because of a more limited pool of suitable AM fungal partners, and this  
72 mechanism is analogous to the indirect eco-evolutionary causes (Pärtel, 2002) (mechanism  
73 three - Fig. 1). Here, we use the term eco-evolutionary processes to describe combined effects  
74 of latitude on phenotypic plasticity, environmental filtering and eco-evolutionary adaptation  
75 of the host plant trait mycorrhizal dependency (e.g. Thuiller *et al.*, 2013). Even though these  
76 different mechanisms are not mutually exclusive, it is important to disentangle how each of  
77 them influences how host plants respond to mycorrhizal symbioses along gradients of latitude  
78 and solar radiation.

79         The benefits that plants receive from the symbiosis in relation to the carbon costs vary  
80 considerably depending on abiotic growth conditions (Johnson *et al.*, 1997; Hoeksema *et al.*  
81 2010; Grman and Robinson, 2013), compatibility of the plant host with the local AM fungal  
82 community (Klironomos, 2003) and the degree to which a plant can take advantage of non-  
83 nutritional functions of mycorrhiza such as protection from pathogens (Veresoglou & Rillig,  
84 2013). Resource stoichiometry of phosphorus (P), nitrogen (N) and light, in particular,  
85 represents a proven tool explaining variance in growth responses of mycorrhizal hosts at  
86 various spatial scales (Johnson, 2010). Latitude-related predictions could complement such  
87 existing tools in understanding why mycorrhizal growth responses differ at large scales. It  
88 may additionally illuminate systematic differences in mycorrhizal responsiveness such as  
89 those explained by the life history of the hosts (Boerner, 1992; Roumet *et al.*, 2005). This  
90 would be the case if the latitudinal effects are mediated through differences in solar radiation.  
91 Annual terrestrial plants may never experience light-duration stress during winter, whereas  
92 the opposite is the case for perennials that represent the majority of terrestrial plants (for  
93 example over 70% of species in the LEDA database are perennials – Kleyer *et al.* 2008).  
94 There is good evidence that perennial AM fungi can survive over winter in the roots of their  
95 hosts (Buwalda *et al.*, 1985; Dodd & Jeffries, 1986 but see Hetrick *et al.*, 1984; Mohammed  
96 *et al.*, 1988), which could affect the carbon economy of their plant hosts. During winter, plant  
97 requirements for nutrients are limited and photoassimilates are in short supply; therefore,  
98 plants that can confine the activity of their mycorrhizal partners may benefit through  
99 improved survival rates. As a result, we expect that there is evolutionary pressure for  
100 perennials to further confine mycorrhizal responsiveness when growing outside the tropics,  
101 compared to annuals.

102

103 We undertook three synthesis activities to establish whether the expectations outlined  
104 above are plausible for mycorrhizal systems (see Methods in supplementary material). We  
105 first compiled a database on crop plant responses to mycorrhiza to identify phenotypic  
106 responses to latitude (Fig. S1). To assess environmental filtering due to AM fungi with  
107 regards to latitude, we synthesized data from a common garden experiment on comparative  
108 mycorrhizal responsiveness of North-American annual and perennial herbaceous plants  
109 (Wilson & Hartnett, 1998) with plant distribution data for the specific plants from USDA  
110 (USDA, 2016). We also tested for differences in mycorrhizal responsiveness across genotypes  
111 of *Zea mays* (maize) that are routinely used either in temperate or tropical systems, despite  
112 that genetic variability could effectively be attributed to breeding. These syntheses activities  
113 were not sufficiently robust to address the mechanistic constituents of the sun worshipper  
114 hypothesis but were carried out to support the over-arching concept and encourage larger  
115 syntheses or experiments exploring the hypothesis in the future.

116 Variance in the database on crop plant responses could be best explained, in our  
117 models consisting of a single predictor, by photosynthetic radiation (Fig 2.a). The optimal  
118 model had an intercept of -0.5 ( $F=9.7$ ,  $P<0.001$ ) and a slope per  $\text{MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  radiation of 0.23  
119 ( $F=6.1$ ,  $P=0.019$ ). Fitted intercepts for the different plant species shared a standard deviation  
120 of 0.048 (Fig. 2a). Analysis of maize lines demonstrated that eco-evolutionary processes also  
121 drive latitude-dependencies on mycorrhizal responsiveness. The Mann-Whitney test between  
122 temperate- (i.e. middle two quartiles) and tropical-climate adapted lines of maize revealed  
123 higher responsiveness for temperate lines ( $U = 24.5$ ,  $P=0.034$ ). When we repeated this  
124 analysis for tropical lines through maintaining the two middle quartiles, the differences  
125 became even more apparent ( $U = 4$ ,  $P<0.001$ , Fig. 2b). Mycorrhizal responsiveness of species  
126 in Wilson and Hartnett (1998) could be predicted by latitude of their distribution, which  
127 suggests that mycorrhizal responsiveness might induce an environmental filtering. We raised  
128 latitude to the fourth power to address fitting issues and obtained an intercept of 0.65; latitude  
129 slope of  $-2.44 \cdot 10^{-8}$  ( $F_{\text{lat}}=23.32$ ;  $P<0.001$ ;  $R^2_{\text{adj}}=0.19$ ; Fig. 2c). We subsequently fitted an  
130 additional parameter that differentiated between annual and perennial plants. Inclusion of the  
131 categorical variable perennial was significant ( $F=23.36$ ,  $P<0.001$ ) and there was a significant  
132 interaction between this parameter and latitude ( $F=9.47$ ,  $P=0.003$ ) suggesting that slopes also  
133 differed. When we analyzed annual and perennial plants separately, we found a significant  
134 relationship only for perennials (Kendall Tau was -0.32 -  $P=0.004$ , whereas for annuals the  
135 Kendall Tau was 0.03 -  $P=0.87$ ).

136 The sun-worshipper hypothesis predicts that latitude impacts mycorrhizal  
137 responsiveness in plants via three complementary mechanisms, namely phenotypic responses,  
138 eco-evolutionary processes and environmental filtering (Fig. 1). Even though the analyses we  
139 report have limited resolution, they were supportive of the sun worshipper hypothesis. We  
140 found evidence that phenotypic plasticity (Fig. 2a), eco-evolutionary processes (Fig. 2b) and  
141 environmental filtering (Fig. 2c) might be operational for all three different types of latitude  
142 related differences in mycorrhizal responsiveness (Thuiller *et al.*, 2013). Despite the findings  
143 from our analyses, it is important to highlight additional factors that may also influence  
144 mycorrhizal responsiveness, and which have the potential to confound our findings. For  
145 example, our observations may correlate with systematic differences in soil fertility; high  
146 weathering rates generally lead to poorer fertility, as occurs in many parts of the tropics (Read  
147 and Perez-Moreno, 2003). Therefore, disentangling the specific role of light versus other  
148 edaphic and environmental factors in driving mycorrhizal responsiveness likely requires  
149 additional experimentation. Testing competing hypotheses could be done with carefully  
150 designed common garden experiments or synthesizing evidence from altitudinal experiments.  
151 Nevertheless, our analysis and associated hypothesis prompts further mechanistic analyses to  
152 test how resource stoichiometry and other critical functions undertaken by mycorrhizal fungi  
153 are influenced by latitudinal gradients.

154

155

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161

### 162 **Contributions**

163 SDV: Conceived the project and carried out the analyses; SDV TH, APM, MCR, AR, DJ:  
164 Discussed and further developed the idea; SDV, DJ: Wrote the manuscript; All authors  
165 commented to the manuscript and approved the final version of it.

166

### 167 **Supplementary Information**

168 Appendix 1: Mycorrhizal dependency as proxy of investment

169 Appendix 2: Meta-analysis on phenotypic plasticity

170 Appendix 3: Eco-evolutionary processes on LGMR

171 Appendix 4: Environmental filtering on LGMR

172 Fig. S1: Locations of the 40 studies included in the meta-analysis

173 Table S1. Primary data on the 42 studies which we considered in our meta-analysis.

174

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251

253 **Legends to Figures**

254

255 Fig. 1. The ‘sun-worshipper’ hypothesis: Light availability declines with latitude ( $x$ -axis) to  
256 which plant species that associate with AM fungi respond via reducing their mycorrhizal  
257 responsiveness (LGMR –  $y$ -axis right). This is depicted in the figure with the black  
258 continuous line describing phenotypic plasticity (Mechanism 1). Eco-evolutionary responses  
259 partially offset the decline in LGMR with latitude (the resulting black discontinuous line has a  
260 lower slope - Mechanism 2). Reduced mycorrhizal responsiveness further induces a decline in  
261 species that associate with AM fungi (red line) with species that either associate with  
262 ectomycorrhizal (ECM) or ericoid (ERM) mycorrhizal fungi (green continuous line –  $y$ -axis  
263 left). This represents Mechanism 3. As a result, latitude is a key factor that determining plant  
264 responsiveness to mycorrhizal fungi

265

266

267 Fig. 2 (a) Scatterplot of mycorrhizal responsiveness plotted against photosynthetic radiation  
268 during the growth period for the annual crops that we included in our crop dataset. The  
269 relationship is positive; (b) beehive plot of mycorrhizal responsiveness of maize lines adapted  
270 to growth under temperate vs tropical conditions. In the plot, we only used the two central  
271 quartiles of the two groups of data. The differences are significant ( $U = 4$ ,  $P < 0.001$ ); (c)  
272 maximum latitude of the distribution of North American herbaceous plants plotted against the  
273 mycorrhizal responsiveness as assayed in a common garden experiment. Each cross describes  
274 the maximum latitude of a single species and the red line is the best fit line for the relationship  
275 with mycorrhizal responsiveness. We found few plants having a high mycorrhizal  
276 responsiveness occurring at high latitudes.



