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1 **Sustainable agriculture: possible trajectories from mutualistic**
2 **symbiosis and plant neodomestication**

3

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5

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15 **Food demand will increase concomitantly with human population.**

16 **Food production therefore needs to be high enough and, at the same**

17 **time, minimize damage to the environment. This equation cannot be**

18 **solved with current strategies. Based on recent findings, new**

19 **trajectories for agriculture and plant breeding which take into account**

20 **the below-ground compartment and evolution of mutualistic strategy,**

21 **are proposed in this opinion article. In this context, we argue that**

22 **plant breeders have the opportunity to make use of native Arbuscular**

23 **Mycorrhizal symbiosis in an innovative ecologically intensive**

24 **agriculture.**

25

26

27

28

29 **A sustainable food production ?**

30 Feeding the world and securing access to food are both major social and

31 scientific issues. Food crises have often occurred in the past. In recent years,

32 the rapidly increasing demand for food (i.e., for human populations and

33 livestock) along with biofuels has led to food price volatility [1]. Furthermore,

34 recent work suggests that food crises are exacerbated by global warming. It

35 has been clearly indicated that agricultural productivity has declined world-

36 wide as a consequence of the hottest summers experienced in the recent past,

37 and according to different global warming scenarios "... *the hottest seasons on*

38 *record will represent the future norm in many locations ...*" [1]. Human
39 population is continuously increasing, but expected to peak before the end of
40 the century, with 10 billion people before 2100 [2]. Contrary to common
41 assumption, non-linearities between population expansion and environmental
42 degradation are likely to increase disproportionately rapidly [3]. Human
43 population expansion will be coupled with an increased demand for space,
44 water and food. These demands will therefore be accompanied by urban and
45 cropland expansion, and more than 10^9 hectares of natural ecosystems are
46 likely to be lost by 2050 [4]. This represents collateral damage for the
47 environment because cropland expansion can only be achieved by replacing
48 non agricultural, mainly forested areas. According to recent studies, agricultural
49 production will have to expand by about 100% during the 21st century to satisfy
50 forecasted world demands [5]. At the same time, agriculture is a major threat
51 to the environment eventually leading to a decline in biodiversity and related
52 ecosystem services, including degradation of soil and water quality [6].

53 A fundamental issue for agriculture during this century is thus to confront
54 two contradictory goals, (i) the need to produce enough food to minimize
55 human malnutrition and support world population expansion and (ii) the need
56 to limit collateral damage to the environment, which can in turn negatively
57 impact agriculture. Based on recent findings about strategies in plant
58 mutualisms and plant selection, we develop new ideas in this paper and
59 suggest trajectories for a more sustainable agricultural development.

60

61 **Intensive vs. extensive agriculture ?**

62 The aim in intensive agriculture is to maximize productivity per unit of surface,

63 whereas in extensive agriculture, lower productivity yields are accepted as a
64 counterpart to less potential ecosystem damage. The main advantage of
65 extensive agriculture is that no or few inputs are required. However this is often
66 countered by a need for a larger soil area to obtain comparable production. It
67 has been shown that agricultural intensification with high yield production
68 eventually increases greenhouse gas emissions per unit surface. However,
69 much higher carbon emissions can be expected if the same production is
70 obtained by expanding low-yield farming (e.g. [7;8]). Similarly, the need to
71 increase agricultural productivity to limit adverse effects on the environment
72 has also been underlined by modeling land use/land cover changes [9] and by
73 projecting possible improvements of productivity in existing agricultural areas
74 [10]. One key element which has emerged is the necessity for agricultural
75 intensification to preserve biodiversity and the related ecosystem services. As
76 developed below, new ideas for maintaining high crop productivity with lower
77 inputs have recently been put forward.

78

79 **Crop selection from traits?**

80 Since the beginning of agriculture, crops have been selected for different traits,
81 including plant productivity. The main current approach to modern plant
82 breeding is to maximize the fitness of individual plants. However other
83 contrasting breeding strategies have been suggested. One of the most exciting
84 of these new solutions would be to base plant breeding on group selection
85 rather than on individual plant fitness [11] (where group selection refers to the
86 selection '*... for attributes that increase total crop yield but reduce plants'*
87 *individual fitness...*' [11]). This would imply a completely new approach to

88 selection criteria. For example, selecting for cooperative shading, which would
89 allow a passive control of weeds, seems promising to improve yield and
90 sustainability [11].

91

92 In all these breeding approaches (i.e. individual selection and group
93 selection), however, plants are always considered as standalone entities, which
94 is arguably a mistake. Plants are deeply dependent on mutualist
95 microorganisms for their growth, and these can be damaged by conventional
96 agricultural practices and current plant breeding strategies.

97

98 **Arbuscular mycorrhiza and consequences of agricultural practices**

99 The arbuscular mycorrhizal symbiosis is responsible for massive global nutrient
100 transfer (Box 1). It is a mutualism 'that helps feed the world' [12]. Arbuscular
101 mycorrhizal fungi, because of their functions, can be considered as key
102 microorganisms for soil productivity.

103 Intensive agricultural management (i.e., conventional agriculture in
104 Europe and North America) has exerted a high selection pressure on
105 microorganisms through profound modification of their habitats and niches,
106 notably brought about by tillage, the high increase of mineral nutrients, and
107 low plant diversity (i.e., crops). Tillage, ploughing and ripping, for example,
108 represent an intense form of soil disruption. In natural habitats, AM mutualism
109 is not subjected to perturbations of this intensity. Such disruption leads to
110 degradation of the hyphal network, ecological functions, and AM fungal
111 diversity [13]. Soil nutrient availability is a strong driving influence for
112 producing an evolved geographic structure in AM mutualism (i.e., a

113 coevolutionary selection mosaic) [14]. As a result, soil fertilization in
114 agricultural ecosystems has had a negative impact on AM fungal functions [15]
115 and diversity [16]. Thus confounding factors, related to conventional
116 agricultural trajectories, likely act synergistically against mycorrhizal symbiosis.

117

118 **Mutualistic strategy and agriculture**

119 From a theoretical point of view, mutualisms (i.e. cooperative interactions
120 among different species) can exhibit instability: individuals potentially benefit
121 from defecting from cooperation if cooperation is costly. Organisms will
122 increase their own fitness, even if this comes to a cost of others. Kiers *et al*,
123 [17] have demonstrated the capacity of plants to sanction less-cooperative
124 strains (i.e. 'cheaters') through a carbon embargo. The gain in fitness for the
125 cheater is therefore reduced by this plant trait. This in itself can explain the
126 stability of this symbiosis. A similar sanction of carbon allocation has been
127 observed in the case of nitrogen-fixing nodules in leguminous plants to control
128 *Rhizobium* cheaters [18]. The most cooperative AM fungal symbionts transfer
129 more phosphorus to the roots when they receive more carbon [17]. Such
130 mutualism is therefore bilaterally controlled because both partners can enforce
131 the cooperation and any possible enslavement strategy is also limited. This
132 fairly explains the stability of arbuscular mycorrhizal symbiosis. In addition, the
133 main advantage for the plant to not enslave its symbionts is the access offered
134 to numerous potential functions harbored by the reservoir of soil AM fungi into
135 which the plant can tap depending on its nutritional requirements. For the
136 fungi, the main advantage of not being enslaved is to be able to maintain a
137 high level of diversity. This symbiosis is one reason for the success of plants in

138 terrestrial ecosystems.

139 Less cooperative AM fungi do exist in nature. We can expect them to
140 become more abundant as the diversity of AM fungi decreases because the
141 symbiotic options offered to the plants are more limited. It has been shown that
142 AM fungi cheaters can develop 'dealer' behavior by keeping phosphorus in
143 polyphosphate chains and delivering it at an expensive cost for the host plant
144 [17]. The plant's capacity to sanction cheaters is a tremendously important
145 trait to maintain, given the fact that most mineral nutrients (~70% of the
146 phosphorus for example) are delivered to plants by AM fungi [19] (Box 1) in
147 'natural' environments.

148

149 **New ideas for more sustainable agricultural practices by promoting** 150 **mutualisms**

151 Ecosystem productivity has been shown to be driven by AM symbiosis
152 diversity [e.g. 20]. Thus, AM fungi constitute a key compartment of soil fertility.
153 The plant can be colonized by a variety of AM fungi (i.e., no host-specificity).
154 However, the recent findings suggest that plants can choose to reward and
155 enroll some fungal colonizers in order to ensure access to particular functions
156 related to their needs [17]. This selective rewarding is likely to lead to the
157 exclusion of certain colonizers and culminate in an observed 'host-plant
158 preference' e.g. [21;22].

159 This leads to the idea that a plant can filter soil AM fungi depending on its
160 requirements, the season and location. Conventional field-based agriculture
161 makes use of very limited crop plant diversity, fungicides, soil tillage and

162 fertilizer. The pressure exerted by agricultural practices leads to a reduction in
163 AM fungal diversity compared to more natural ecosystems e.g. [23;24].
164 Breeders generally select crop cultivars from rich soils which have been under
165 conventional agriculture for many years. In fact, the ultimate result of this
166 selection strategy is to produce a plant that is best adapted to current
167 agricultural practices and the related agrosystems anthropization. Agricultural
168 soils have been enriched with fertilizers for decades and the ecological function
169 of AM fungi as plant phosphorus providers is less important in these enriched
170 soils. This, together with the breeding trajectory, will have relaxed the plant
171 sanction trait in modern crops, as is the case in soybean (*Glycine max* (L.)
172 Merr.) where ancient varieties are better able to control *Rhizobia* cheaters than
173 modern ones [18]. From an interesting meta-analysis performed from 39
174 publications it appears that there is '*...no evidence that new crops plant*
175 *genotypes lost their ability to respond to mycorrhiza due to agricultural and*
176 *breeding practices...*' [25].

177 Two alternative hypotheses for AM symbiosis can be put forward. First, we
178 can hypothesize that the same trend as in the *Rhizobium*/legume mutualism
179 will have already occurred for AM mutualism with a resulting loss of the
180 sanction trait against AM fungal cheaters. As a consequence, an increase in AM
181 fungal cheaters can be expected in agricultural soils. Because AM fungi
182 constitute a fundamental component of soil fertility, solutions for a more
183 ecologically intensive agriculture should focus on this compartment (Box 2.).
184 Plant breeders could also imagine new selection trajectories where the sanction
185 trait is considered as a major selection target (i.e. the capacity of plants to
186 punish bad cooperators by a carbon embargo [17]). In this way the possibilities

187 offered by AM functional efficiency could be restored and agricultural practices
188 modified by reducing soil inputs and tillage (Box 2). The alternative hypothesis
189 is that plant breeders have selected cultivars that are very efficient for mineral
190 foraging through soil AM fungal mutualists. This apparently optimistic
191 hypothesis is worse than that of a loss of the sanction trait in crops, because of
192 the lack of long term sustainability. Furthermore, one important component of
193 soil fertilizer, phosphorus, is known to rely on high quality rock phosphate,
194 which is a finite resource. More than 85% of the global phosphate resources are
195 dominated by only 3 countries which is far fewer than the number of countries
196 controlling the world's oil reserves [26]. Phosphorus (P) supply is thus of
197 strategic importance for many countries, and “...many food producers are in
198 danger of becoming completely dependent on this trade...” [26]. Major
199 agricultural regions such as India, America, and Europe are already dependent
200 on P imports. Phosphate market prices can soar, as shown by the 700%
201 increase in 2008 [26], especially as phosphate mining production is predicted
202 to attain a peak in 2030 [27].

203

204 Other plant mutualisms, in addition to arbuscular mycorrhiza, should
205 potentially have a synergistic impact on plant productivity and plant resistance
206 against stresses (Box 2). For example, infection of barley (*Hordeum vulgare*)
207 with an endophytic fungus, *Piriformosa indica*, increases resistance to stresses
208 including salinity and systemic resistance of the crop to root and leaf
209 pathogens, and a concomitant increase in yield production [28]. Native plants
210 in coastal environments and geothermal habitats require fungal endophytes in
211 order to grow [29]. Thus a passive adaptation of the plant is observed, with the

212 endophytic fungus providing a selective advantage to the colonized plant.
213 Infection of the tomato (*Solanum lycopersicum*) plant with these endophytes,
214 for example, confers salt or heat resistance [29]. It can thus be argued that
215 solutions, which support a more productive and sustainable agriculture and
216 involve the use of endophytic microorganisms, do exist but have as yet been
217 little explored.

218

219 **Concluding remarks**

220 The Green Revolution that started about 50 years ago, allowed food shortages
221 to be limited. Given the stocks of resources and human population growth, this
222 Green Revolution can continue for only a few more decades. The counterpart of
223 this Green Revolution is a high cost to the environment and global
224 environmental changes [4]. If nothing is done to counteract these changes,
225 thresholds will be exceeded, with dramatic consequences [3] and indeed the
226 impossibility for natural ecosystems to regenerate. A more sustainable
227 agriculture and a plant neodomestication has to emerge to guarantee food
228 supply over the next 50 years. One way of achieving a more ecologically
229 intensive agriculture would be to consider and protect the ecological functions
230 displayed by AM fungi, which have been effective for more than 400 million
231 years, whatever the ecosystem. This will not only improve natural plant mineral
232 nutrition but also water supply and other ecological functions that have already
233 been clearly documented [30]. Research efforts must also
234 stimulate/accompany this possible plant neodomestication.

235

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239 and suggestions of modifications on previous versions of the manuscript.

240 **Box 1. Arbuscular mycorrhizal symbiosis**

241 Among plant mutualistic symbioses, the arbuscular mycorrhiza relationship has
242 been evolving for more than 400 million years [31]. This symbiosis is really
243 mundane and widespread with approximately 80% of land plants colonized by
244 AM fungi [30] across a huge diversity of ecosystems. In this symbiosis, plants
245 provide carbohydrates to the arbuscular mycorrhizal fungi in exchange for
246 minerals, drought resistance and protection against pathogens e.g. [30;32].
247 The fungus in this mutualistic relationship is an obligate biotroph, its
248 transmission is horizontal and there is no genetic uniformity between fungal
249 symbionts. Several different fungal symbionts colonize the same plant roots.

250

251

252 **Box 2. Future of agricultural trajectories guidelines**

253 Forests represent important carbon stocks which, when converted into
254 agrosystems, have a huge impact on CO₂ emission to the atmosphere [33] as
255 well as a collateral effect on biodiversity [6;9]. In the context of global changes,
256 it seems fundamental to limit agricultural expansion [10]. The key point seems
257 to be to improve crop yields within existing agrosystems. However,
258 conventional agricultural practices and plant breeding strategies have arguably
259 entered a 'cul-de-sac' because they are “...*unlikely to improve attributes*
260 *already favored by millions of years of natural selection...*” [11] while under-
261 explored natural keys to crop yield improvement, such as AM fungi, exist but
262 are ignored and maltreated.

263 To maintain or restore this essential component of soil fertility,
264 conventional agricultural practices need to be modified. The following are
265 suggested guidelines to improve the sustainability of human land use and crop
266 productivity:

267 (i) Because AM diversity is positively correlated with plant diversity e.g. [20],
268 agriculture will need to make use of greater plant diversity.

269 (ii) Tillage, if employed, will need to be restricted to maintain hyphal networks
270 and functional efficiency and also to preserve soil aggregates and limit water
271 losses [34].

272 (iii) Plant breeders should select plants in poor soils, taking into account the
273 two previous aspects, the aim being to maximize the efficiency of AM fungi
274 symbiosis (i.e., plants able to take full advantage of the AM fungi available in

275 soils). These new selected plants might also be able to restore effective AM
276 fungi in the field

277 (iv) Additional mutualist microorganisms such as endophytic fungi should also
278 be considered as important targets to improve plant resistance and
279 productivity.

280

281 This should facilitate a passive promotion of AM fungal mutualism and, at
282 the same time, reduce the use of fertilizers, biocides and water. These
283 guidelines have the potential to enhance crop yields and reduce the problems
284 associated with conventional agriculture in both developed and developing
285 countries.

286

287

288

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366 Netherlands

367

368 **Figure 1**

369 Hyphal network of arbuscular mycorrhiza. This dense network propagated from
370 the plant roots explores a high volume of soil and capture mineral nutrients and
371 water which are transfered to the roots to the benefit of the host-plant. In
372 return host-plant provides photosynthesized sugars and polylosides to sustain
373 the mutualistic fungal compartment.

374