

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

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4 **Marie Duhamel<sup>1,2</sup>, Philippe Vandenkoornhuyse<sup>1</sup>.**

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6 <sup>1</sup>Université de Rennes I, CNRS UMR6553 EcoBio, Campus Beaulieu, F-35042  
7 Rennes, France.

8 <sup>2</sup>Institute of Ecological Science, Vrije Universiteit, 1081 HV Amsterdam,  
9 Netherlands

10 *Corresponding author:* Prof P. Vandenkoornhuyse  
11 (philippe.vandenkoornhuyse@univ-rennes1.fr)

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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.**

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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 21<sup>st</sup> 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.

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### 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.

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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 CO<sub>2</sub> 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.

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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