

# Sustainable agriculture: possible trajectories from mutualistic symbiosis and plant neodomestication

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- Sustainable agriculture: possible trajectories from mutualistic
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- 3

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Food demand will increase concomitantly with human population. 15 Food production therefore needs to be high enough and, at the same 16 time, minimize damage to the environment. This equation cannot be 17 solved with current strategies. Based on recent findings, new 18 trajectories for agriculture and plant breeding which take into account 19 20 the below-ground compartment and evolution of mutualistic strategy, are proposed in this opinion article. In this context, we argue that 21 22 plant breeders have the opportunity to make use of native Arbuscular Mycorrhizal symbiosis in an innovative ecologically 23 intensive 24 agriculture.

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#### 29 A sustainable food production ?

Feeding the world and securing access to food are both major social and 30 scientific issues. Food crises have often occurred in the past. In recent years, 31 the rapidly increasing demand for food (i.e., for human populations and 32 livestock) along with biofuels has led to food price volatility [1]. Furthermore, 33 recent work suggests that food crises are exacerbated by global warming. It 34 has been clearly indicated that agricultural productivity has declined world-35 36 wide as a consequence of the hottest summers experienced in the recent past, and according to different global warming scenarios "... the hottest seasons on 37

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

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

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

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#### 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 breeding is to maximize the fitness of individual plants. However other 82 contrasting breeding strategies have been suggested. One of the most exciting 83 of these new solutions would be to base plant breeding on group selection 84 rather than on individual plant fitness [11] (where group selection refers to the 85 selection '... for attributes that increase total crop yield but reduce plants' 86 individual fitness...' [11]). This would imply a completely new approach to 87

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

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

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#### 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.

Intensive agricultural management (i.e., conventional agriculture in 103 104 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 low plant diversity (i.e., crops). Tillage, ploughing and ripping, for example, 107 represent an intense form of soil disruption. In natural habitats, AM mutualism 108 is not subjected to perturbations of this intensity. Such disruption leads to 109 degradation of the hyphal network, ecological functions, and AM fungal 110 diversity [13]. Soil nutrient availability is a strong driving influence for 111 producing an evolved geographic structure in AM mutualism (i.e., a 112

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

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

138 terrestrial ecosystems.

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

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

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

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

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

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

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

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204 Other plant mutualisms, in addition to arbuscular mycorrhiza, should potentially have a synergistic impact on plant productivity and plant resistance 205 206 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 in coastal environments and geothermal habitats require fungal endophytes in 210 order to grow [29]. Thus a passive adaptation of the plant is observed, with the 211

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.

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#### 219 Concluding remarks

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

235

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#### 240 Box 1. Arbuscular mycorrhizal symbiosis

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

250

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

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

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

(ii) Tillage, if employed, will need to be restricted to maintain hyphal networks
and functional efficiency and also to preserve soil aggregates and limit water
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

soils). These new selected plants might also be able to restore effective AMfungi in the field

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

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

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#### 289 **References**

- 1 Battisti, D.S. and Naylor, R.L. (2009) Historical warnings of future food
   insecurity with unprecedented seasonal heat. *Science* 323,240-244
- 292 2 Lutz, W. *et al.* (2001) The end of world population growth. *Nature* 412, 543293 545
- 3 Harte, J. (2007) Human population as a dynamic factor in environmental
   degradation. *Popul. Environ.* 28, 223-236
- 4 Tilman, D. *et al.* (2001) Forecasting agriculturally driven global environmental
   change. *Science* 292,281-284
- 298 5 Cirera, X. and Masset, E. (2010) Income distribution trends and future food 299 demand. *Phil. Trans. R. Soc. B* 365,2821-2834
- 300 6 Foley, J.A. *et al.* (2005) Global consequences of land use. *Science* 309, 570 301 574
- 302 7 Burney, J.A. *et al.* (2010) Greenhouse gas mitigation by agricultural
   303 intensification. *Proc. Natl. Acad. Sci. U.S.A.* 107,12052-12057
- 304 8 Balmford, A. *et al.* (2012) What conservationists need to know about farming.
   305 *Proc. R. Soc. B.* 279,2714-2724

306 9 Nelson, E. *et al.* (2010) Projecting global land-use change and its effect on

307 ecosystem service provision and biodiversity with simple models. *PloS ONE* 

308 5, e14327 doi:10.1371/journal.pone.0014327 (http://www.plosone.org/)

10 Foley, J.A. et al. (2011) Solution for a cultivated planet. Nature 478, 337-342

310 11 Weiner, J. et al. (2010) Evolutionary agroecology, the potential for

311 cooperative, high density, weed-suppressing cereals. *Evol. Appl.* 3,473-479

- 12 Marx, J. (2004) The roots of plant-microbe collaborations. *Science* 304, 234236
- 13 Verbruggen, E. and Kiers E.T. (2010) Evolutionary ecology of mycorrhizal
   functional diversity in agricultural systems. *Evol. Appl.* 3,547-560
- 316 14 Johnson, N.C. *et al.* (2010) Resource limitation is a driver of local adaptation
- in mycorrhizal symbioses. *Proc. Natl. Acad. Sci. U.S.A.* 107, 2093-2098
- 318 15 Johnson, N.C. (1993) Can fertilization of soil select less mutualistic
  319 mycorrhizae. *Ecol. Appl.* 3, 749-757
- 16 Egerton-Warburton, L.M. *et al.* (2007) Mycorrhizal community dynamics
   following nitrogen fertilization, a cross-site test in five grasslands. *Ecol. Monogr.* 77, 527-544
- 323 17 Kiers, E.T. *et al.* (2011) Reciprocal rewards stabilize cooperation in the
   324 mycorrhizal symbiosis. *Science* 333, 880-882
- 325 18 Kiers, E.T. *et al.* (2007) Human selection and the relaxation of legume
   326 defences against ineffective rhizobia. *Proc. Natl. Acad. Sci. U.S.A.* 274,3119 327 3126
- 19 Smith, S.E. *et al.* (2003) Mycorrhizal fungi can dominate phosphate supply
   to plants irrespective of growth responses. *Plant Physiol.* 133, 16-20
- 20 van der Heijden, M.G.A. *et al.* (1998) Mycorrhizal fungal diversity determines
   plant biodiversity, ecosystem variability and productivity. *Nature* 396, 69–72
- 332 21 Vandenkoornhuyse, P. et al. (2002) Arbuscular mycorrhizal community
- 333 composition associated with two plant species in a grassland ecosystem.
- 334 *Mol. Ecol.* 11,1555-1564

22 Vandenkoornhuyse, P. et al. (2003) Co-existing grass species have 335 distinctive arbuscular mycorrhizal communities. Mol. Ecol. 12, 3085-3095 336 23 Helgason, T. et al. (1998) Ploughing up the wood-wide web? Nature 394,431. 337 24 Verbruggen, E. et al. (2010) Positive effects of organic farming on below-338 339 around mutualists. large-scale comparison of mycorrhizal fungal 340 communities in agricultural soils. New Phytol. 186, 968-979

341

25 Lehman, A. *et al.* (2012) Mycorrhizal responsiveness trends in annual crop
plants and their wild relatives – a meta-analysis on studies from 1981 to
2010. *Plant Soil* 355, 231-250.

345 26 Elser, J. and Bennett, E. (2011) A broken biogeochemical cycle. *Nature*346 478,29-31

27 Cordell, D. *et al.* (2009) The story of phosphorus, global food security and
food for thought. *Global Environ. Chang.* 19, 292-305

Waller, F. *et al.* (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher
 yield. *Proc. Natl. Acad. Sci. U.S.A.* 102, 13386-13391

352 29 Rodriguez, R.J. *et al.* (2008) Stress tolerance in plants via habitat-adapted
 353 symbiosis. *ISME J.* 2, 404-416

30 Smith, S. and Read, D. (2008) Mycorrhizal Symbiosis, Edition 3. Academic
 Press and Elsevier London ISBN 978-0-12-370526-6

356 31 Redecker, D. *et al.* (2000) Glomalean fungi from the Ordovician. *Science* 357 289, 1920-1921

358 32 Smith, S.E. *et al.* (2010) Plant performance in stressful environments, 359 interpreting new and established knowledge of the roles of arbuscular 360 mycorrhizas. *Plant Soil* 326, 3-20

33 Aldhous, P. (2004) Land remediation: Borneo is burning. *Nature* 432, 144 146

363 34 De Souza Andrade, D. *et al.* (2003) Long-term effects of agricultural 364 practices on microbial community. In *Conservation agriculture.* (García-365 Torres, L. *et al.* eds.), pp. 301-306 Kluwer Academic Publishers, Dordrecht, 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.