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Sustainable agriculture: possible trajectories from mutualistic symbiosis and plant neodomestication

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

A sustainable food production ?

Feeding the world and securing access to food are both major social and scientific issues. Food crises have often occurred in the past. In recent years, the rapidly increasing demand for food (i.e., for human populations and livestock) along with biofuels has led to food price volatility [1]. Furthermore, recent work suggests that food crises are exacerbated by global warming. It has been clearly indicated that agricultural productivity has declined world-wide as a consequence of the hottest summers experienced in the recent past, and according to different global warming scenarios "… *the hottest seasons on* *record will represent the future norm in many locations* ...” [1]. Human population is continuously increasing, but expected to peak before the end of the century, with 10 billion people before 2100 [2]. Contrary to common assumption, non-linearities between population expansion and environmental degradation are likely to increase disproportionately rapidly [3]. Human population expansion will be coupled with an increased demand for space, water and food. These demands will therefore be accompanied by urban and cropland expansion, and more than 10^9 hectares of natural ecosystems are likely to be lost by 2050 [4]. This represents collateral damage for the environment because cropland expansion can only be achieved by replacing non agricultural, mainly forested areas. According to recent studies, agricultural production will have to expand by about 100% during the 21st century to satisfy 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 ecosystem services, including degradation of soil and water quality [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.

Intensive vs. extensive agriculture ?

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

Crop selection from traits?

Since the beginning of agriculture, crops have been selected for different traits, including plant productivity. The main current approach to modern plant breeding is to maximize the fitness of individual plants. However other contrasting breeding strategies have been suggested. One of the most exciting of these new solutions would be to base plant breeding on group selection rather than on individual plant fitness [11] (where group selection refers to the selection '... *for attributes that increase total crop yield but reduce plants*' *individual fitness*...' [11]). This would imply a completely new approach to selection criteria. For example, selecting for cooperative shading, which would allow a passive control of weeds, seems promising to improve yield and sustainability [11].

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.

Arbuscular mycorrhiza and consequences of agricultural practices

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

Intensive agricultural management (i.e., conventional agriculture in Europe and North America) has exerted a high selection pressure on microorganisms through profound modification of their habitats and niches, notably brought about by tillage, the high increase of mineral nutrients, and low plant diversity (i.e., crops). Tillage, ploughing and ripping, for example, represent an intense form of soil disruption. In natural habitats, AM mutualism is not subjected to perturbations of this intensity. Such disruption leads to degradation of the hyphal network, ecological functions, and AM fungal diversity [13]. Soil nutrient availability is a strong driving influence for producing an evolved geographic structure in AM mutualism (i.e., a coevolutionary selection mosaic) [14]. As a result, soil fertilization in agricultural ecosystems has had a negative impact on AM fungal functions [15] and diversity [16]. Thus confounding factors, related to conventional agricultural trajectories, likely act synergistically against mycorrhizal symbiosis.

Mutualistic strategy and agriculture

From a theoretical point of view, mutualisms (i.e. cooperative interactions among different species) can exhibit instability: individuals potentially benefit from defecting from cooperation if cooperation is costly. Organisms will increase their own fitness, even if this comes to a cost of others. Kiers *et al,* [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 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 observed in the case of nitrogen-fixing nodules in leguminous plants to control *Rhizobium* cheaters [18]. The most cooperative AM fungal symbionts transfer more phosphorus to the roots when they receive more carbon [17]. Such mutualism is therefore bilaterally controlled because both partners can enforce the cooperation and any possible enslavement strategy is also limited. This fairly explains the stability of arbuscular mycorrhizal symbiosis. In addition, the main advantage for the plant to not enslave its symbionts is the access offered to numerous potential functions harbored by the reservoir of soil AM fungi into which the plant can tap depending on its nutritional requirements. For the fungi, the main advantage of not being enslaved is to be able to maintain a high level of diversity. This symbiosis is one reason for the success of plants in terrestrial ecosystems.

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 symbiotic options offered to the plants are more limited. It has been shown that AM fungi cheaters can develop 'dealer' behavior by keeping phosphorus in 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 trait to maintain, given the fact that most mineral nutrients (~70% of the phosphorus for example) are delivered to plants by AM fungi [19] (Box 1) in 'natural' environments.

New ideas for more sustainable agricultural practices by promoting mutualisms

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

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

Two alternative hypotheses for AM symbiosis can be put forward. First, we can hypothesize that the same trend as in the *Rhizobium*/legume mutualism will have already occurred for AM mutualism with a resulting loss of the sanction trait against AM fungal cheaters. As a consequence, an increase in AM fungal cheaters can be expected in agricultural soils. Because AM fungi constitute a fundamental component of soil fertility, solutions for a more ecologically intensive agriculture should focus on this compartment (Box 2.). Plant breeders could also imagine new selection trajectories where the sanction trait is considered as a major selection target (i.e. the capacity of plants to punish bad cooperators by a carbon embargo [17]). In this way the possibilities offered by AM functional efficiency could be restored and agricultural practices 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 foraging through soil AM fungal mutualists. This apparently optimistic hypothesis is worse than that of a loss of the sanction trait in crops, because of the lack of long term sustainability. Furthermore, one important component of soil fertilizer, phosphorus, is known to rely on high quality rock phosphate, which is a finite resource. More than 85% of the global phosphate resources are 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 strategic importance for many countries, and “...*many food producers are in danger of becoming completely dependent on this trade*...” [26]. Major agricultural regions such as India, America, and Europe are already dependent on P imports. Phosphate market prices can soar, as shown by the 700% increase in 2008 [26], especially as phosphate mining production is predicted to attain a peak in 2030 [27].

Other plant mutualisms, in addition to arbuscular mycorrhiza, should potentially have a synergistic impact on plant productivity and plant resistance against stresses (Box 2). For example, infection of barley (*Hordeum vulgare*) with an endophytic fungus, *Piriformosa indica*, increases resistance to stresses including salinity and systemic resistance of the crop to root and leaf pathogens, and a concomitant increase in yield production [28]. Native plants in coastal environments and geothermal habitats require fungal endophytes in order to grow [29]. Thus a passive adaptation of the plant is observed, with the endophytic fungus providing a selective advantage to the colonized plant. Infection of the tomato (*Solanum lycopersicum*) plant with these endophytes, for example, confers salt or heat resistance [29]. It can thus be argued that solutions, which support a more productive and sustainable agriculture and involve the use of endophytic microorganisms, do exist but have as yet been little explored.

Concluding remarks

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

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Box 1. Arbuscular mycorrhizal symbiosis

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

Box 2. Future of agricultural trajectories guidelines

Forests represent important carbon stocks which, when converted into 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, it seems fundamental to limit agricultural expansion [10]. The key point seems to be to improve crop yields within existing agrosystems. However, conventional agricultural practices and plant breeding strategies have arguably entered a 'cul-de-sac' because they are "...*unlikely to improve attributes already favored by millions of years of natural selection*..." [11] while under-explored natural keys to crop yield improvement, such as AM fungi, exist but are ignored and maltreated.

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:

(i) Because AM diversity is positively correlated with plant diversity e.g. [20], 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].

(iii) Plant breeders should select plants in poor soils, taking into account the two previous aspects, the aim being to maximize the efficiency of AM fungi 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 AM fungi in the field

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

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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Figure 1

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