Letter

Why farmers should manage the arbuscular mycorrhizal symbiosis

A response to Ryan & Graham (2018) 'Little evidence that farmers should consider abundance or diversity of arbuscular mycorrhizal fungi when managing crops'

The Tansley review by Ryan & Graham (2018) provided a welcome critical perspective on the role of arbuscular mycorrhizal (AM) fungi in large-scale industrial agriculture, with a focus on cereals (wheat, *Triticum aestivum*). They conclude that there is little evidence that farmers should consider the abundance or diversity of AM fungi when managing crops. We welcome many of the points made in the paper, as they give an opportunity for self-reflection, considering that the importance of AM fungi in agroecosystems is often taken for granted. However, we suggest that it is too early to draw the overall conclusion that the management of AM fungi by farmers is currently not warranted.

We offer the following points to contribute to the discussion. The first point pertains to the overall focus of Ryan & Graham (2018), which strongly determines the recommendations at which the authors arrive. This scope is limited to yield, at the expense of neglecting aspects of sustainability. We then argue that AM fungal communities do respond negatively to aspects of agricultural management, and list evidence for their positive effects to agronomically important traits, including yield in cereals. In our final argument, we advocate for transitioning to agroecosystems that are more AM compatible in order to increasingly take advantage of all the potential services these ancient symbionts, and other soil biota, can provide.

AM fungi are not just important for yield, but also for system performance and sustainability

Given the need to feed more people and to do so without limiting options for the future and jeopardizing our soils and the environment, a perspective that focuses only on yield is very limited, as Ryan & Graham (2018) also discuss. Yield is certainly important, and translates to income for the farmer and low price for the consumer, and so it is a crucial component in the short term; however, it is not the only factor to consider, especially when it comes to long-term sustainability and yield stability of agroecosystems. In their earlier analysis (Ryan & Graham, 2002), coming to similar overall conclusions, one point was also highlighted: the role of these fungi in soil aggregation. AM fungi (Leifheit *et al.*, 2014) and other soil biota as well (Lehmann *et al.*, 2017) make important contributions to soil structure, a key ecosystem parameter that relates to sustainable management. We propose that, even if there is little evidence that AM fungi contribute to the yield of certain crops, it would still be worth implementing management practices favoring AM fungi because of AM fungal contributions to many other ecosystem functions (Powell & Rillig, 2018). Such functions, potentially relevant also in the field, include soil aggregation (Rillig *et al.*, 2016) and reduced nutrient losses (Cavagnaro *et al.*, 2015). Furthermore, AM fungi have also been shown to enhance the temporal stability of plant community productivity in grasslands (Yang *et al.*, 2014), indicating the potential role in yield stability when faced with a changing environment. Another aspect is yield quality (e.g. biofortification of the grains), which can be enhanced by AM fungi (e.g. Lehmann *et al.*, 2014; Bona *et al.*, 2017; Torres *et al.*, 2018). Indeed, AM fungi may have contributions 'from field to fork', that is also after harvest, e.g. enhancing food storage properties (Rillig *et al.*, 2018). Finally, improvements in plant nutrient acquisition, even in the absence of a yield increase, may reduce the amounts of fertilizer required to achieve the same yield, thereby affecting profitability.

AM fungal diversity and abundance respond negatively to industrial agricultural management practices

Ryan & Graham (2018) review some of the key agricultural interventions and provide evidence of a limited effect of these factors on AM fungi, when examined individually. We believe this analysis runs the risk of oversimplification of what is known as a very complex issue, for several reasons. (1) Although such management practices in isolation may have limited impacts (especially on a potentially already reduced AM fungal community), this single-factor approach does not capture the reality on an agricultural field. Instead, what AM fungal communities encounter is the combination of multiple management practices, including fertilization, agrochemical use, tillage, host plant and other cropping practices. (2) Ryan & Graham (2018) do not include agrochemical effects in this discussion. However, fungicides (foliar applications and seed treatments) can reduce AM fungal spore germination, mycorrhiza formation, AM fungal community composition, extraradical hyphae and/or spore production (Dodd & Jeffries, 1989; Merryweather & Fitter, 1996; Wilson & Williamson, 2008; Hernandez-Dorrego & Mestre-Pares, 2010; Ipsilantis *et al.*, 2012; Jin *et al.*, 2013; Buysens *et al.*, 2015; Lekberg *et al.*, 2017). (3) Plant breeding in the future should occur in environments that favor interactions of plants and AM fungi (reviewed in Bennett *et al.*, 2013). Currently available plant varieties have not been directly selected to engage in symbioses, partly as a result of common farming practices during the selection process that usually apply fungicides and the relatively high and easily available amounts of phosphorus (P). Even breeding programs that limit P availability (to focus on P use efficiency) do not necessarily select for plants colonized by AM fungi and thus might miss out on the benefits of AM fungi other than P mobilization, such as drought and disease resistance. We propose to also focus on mycorrhiza use efficiency (MUE; also see next section). (4) Recent results using molecular ecology tools, which can also capture nonsporulating AM fungal genotypes (by contrast with the spore-based evidence selected by Ryan & Graham (2018)), have clearly shown a decreasing diversity trend with time since sites were under area-typical management (Roy *et al.*, 2017). Similarly, several studies have shown that AM fungal community structure is strongly affected by agricultural practices. For example, comparing agricultural systems with adjacent grassland vegetation, it seems that certain AM fungal genotypes with potentially desirable trait combinations (linked to high nitrogen (N) : P ratios) are selectively lost once under the agricultural regime (Verbruggen *et al.*, 2015). In fact, Ryan & Graham (2018) acknowledge similar evidence, but regard it as secondary, because, in their examples, this shift in community structure did not translate into yield. As the functionality and role of diversity in AM fungi is not completely resolved (Powell & Rillig, 2018), we feel it would be premature to assume that shifts in community composition will remain without detrimental consequences in agroecosystems.

Evidence of AM fungal roles in enhancing cereal yield in the field

Clearly, there are many crops for which AM fungi have been convincingly shown to increase yield, including cassava (Ceballos *et al.*, 2013; Rodriguez & Sanders, 2015) and potato (Hijri, 2016). The authors focus mostly on cereals (mostly wheat), which is legitimate, as long as recommendations reflect this limitation. The overall conclusion of Ryan & Graham (2018) is potentially misleading, as they largely focus on cereals, crops that are known to have poor or intermediate responsiveness to AM fungi, probably because they usually have a fine root system. In their paper, the authors exclude inoculation studies from their discussion of yield-enhancing effects, because this is not a viable management option for cereals (because of economic concerns, among others). We partly agree with this latter notion; however, the exclusion of this body of literature is problematic when it comes to establishing the causality of AM fungal effects, because, so far, this is one of the best options for the experimental detection of causality in complex field conditions. Moreover, a number of companies are now testing whether seed coating is a suitable method to inoculate AM fungi. This method is economically feasible for widespread application, as relatively small amounts of inoculum are needed. Hence, if this application method is an efficient way to enhance the abundance of AM fungi in the field, and has beneficial effects, it will become a viable tool for application. Ryan & Graham (2018) criticize studies not based on inoculation, which only very indirectly reduce AM fungal inoculum (e.g. fallow), and which have multiple other effects, for not sufficiently providing evidence of AM fungal contributions. We believe that it is important to clearly acknowledge that AM fungal inoculation studies can serve the purpose of providing opportunities to show causation (by directly manipulating the factor in question), irrespective of whether one would recommend inoculation as a management practice. When including the literature based on inoculation experiments, it is clear that AM fungi can increase the yield of crops, even cereals such as wheat (e.g. Mäder *et al.*, 2011).

Ryan & Graham (2018) highlight two crucial factors that compromise their own main conclusion ('management of AM fungi by farmers will not be warranted'): (1) the methodology used for the quantification of mycorrhiza in many past studies; and (2) the existence of a cost–benefit optimum of the AM fungal symbiosis (trade balance). Most field studies have quantified AM fungi on the basis of the root length colonized, instead of arbuscules and external hyphae. However, even if arbuscules are measured, the trade balance (MUE) dictates the benefit (see Hohmann & Messmer, 2017). Other studies have been based on spore counts as a proxy for diversity, but spores are not always a reliable indicator of AM fungi. Thus, we feel that it is risky to ignore the many contributions of AM fungi solely because we do not see a correlation between AM fungal abundance using conventional methods and yield. Instead, farmers should be given the possibility, as part of their management options, to choose symbiosis-efficient plant varieties.

Although there is a fair amount of evidence of positive AM fungal effects from a range of crops, it is still a fair point to argue that disentangling the actual contribution of AM fungi in realistic field situations is extremely challenging. This situation is actually no different from natural ecosystems (Powell & Rillig, 2018); if anything, the situation in agroecosystems is perhaps slightly better because of inoculation trials. A range of tools can be applied to better study complex agroecosystems, including the use of mutants and other genetic resources with known differences in mycorrhizal responsiveness. Although mutants are currently lacking for cereals, they have been used to gain valuable insights into other agricultural systems. For example, a mycorrhiza-defective tomato mutant and its mycorrhizal wild-type progenitor have been used under field (and laboratory) conditions to explore the benefits of AM fungi. Interestingly, although, in many of these studies, an increase in yield was not found, there was a strong (positive) nutritional response (for a review, see Watts-Williams & Cavagnaro, 2014). This finding highlights the importance of how we express mycorrhizal benefits: is it in terms of yield, nutrient acquisition and/or profitability?

Existing agroecosystems may not be optimal: what is an appropriate frame of reference?

Large-scale production agriculture clearly 'works' in terms of feeding the world. However, the trade-offs in terms of sustainability are still not fully resolved and the long-term consequences of intensive agriculture (e.g. reduced soil quality, reduced soil biodiversity, high nutrient losses through leaching and denitrification, pollution of drinking water with nitrate, enhanced soil erosion) are often not accounted for. Under this current paradigm, referred to by Ryan & Graham (2018) as the agronomic perspective, AM fungal communities, as well as other soil biota, probably do not, and cannot, function well (see earlier section on

Table 1 High-priority research questions for understanding the role of arbuscular mycorrhizas (AMs) in agriculture and for transitioning to AM-adequate agricultural systems; we give approximate time horizons for addressing these questions.

Research question	Research focus/development	Time horizon
Are there critical thresholds for mycorrhizal functioning in agroecosystems along gradients of agricultural management and different climatic and pedological context?	Assess impacts of multiple agricultural practices Improved methodology to analyze AM functionality	> 10 yr
What are the trait profiles of AM fungal genotypes that are lost during agroecosystem establishment/management?	Enlarge databases of AM fungal traits	5–10 yr
What are suitable indicators/parameters in soil and roots that best represent an efficient use of AM fungi? Which easy-to-use tools can we develop that will allow farmers and breeders to quickly assess beneficial plant–AM fungal interactions?	Develop rapid tools to assess plant–AM fungal interactions, e.g. phytometer systems, AM fungal indicator species	> 10 yr
Are there trade-offs between yield and system performance effects (e.g. soil aggregation, soil erosion, nutrient cycling) mediated by the AM fungal community? Are there trade-offs in AM fungal functioning within a crop rotation (i.e. how to enhance AM fungal benefits for crops belonging to different functional groups)?	Meta-analyses evaluating this topic More functional ecological studies in various agricultural systems Temporally intensive monitoring (cheap and high-throughput)	> 10 yr
How can we manage gradual transitions towards more AM-adequate agricultural systems, considering socio-economic factors and without jeopardizing food security? What other soil biota should be considered together with AM fungi in these agricultural transitions?	Large-scale research consortia integrating soil ecology, agronomy, economics	> 10 yr
Can we develop mycorrhiza-defective cereal mutants that – as 'sentinel plants' – allow for AM functioning to be assessed in the field?	Mutant screening and method development	5–10 yr
Can AM fungi increase the temporal stability of crop yields by providing multiple benefits in the field?	Long-term agricultural field experiments Exploitation of existing databases	5–10 yr
How can we predict under which conditions and with which crop genotypes AM management is economically and environmentally beneficial?	Field inoculation studies (incl. seed coating) Promoting management practices that enhance AM fungal abundance Socio-economic analyses	> 10 yr

'AM fungal diversity and abundance respond negatively to industrial agricultural management practices'). Therefore, it is perhaps 'unfair' to say that AM fungi do not perform adequately and thus should not be a target of management. Perhaps the agricultural paradigm should be changed to allow AM fungi and other soil biota to function better; the path to such a change is certainly complicated, but should involve the inclusion of AM fungi (and other beneficial soil biota) explicitly in management decisions, rather than ignoring them. Even if we agreed with all the conclusions presented in Ryan & Graham (2018), we would still propose to redesign a system that is currently not beneficial for AM fungi and many other soil organisms. This idea of redesigning systems that promote beneficial soil biota, such as AM fungi, is not new (see the large literature on agroecology; for example, Wezel *et al.*, 2013; Bender *et al.*, 2016; DeClerck *et al.*, 2016), and is based on the enhancement of ecosystem services to boost sustainable agricultural production.

Conclusions

In summary, we believe that Ryan & Graham (2018) have brought a much-needed push to critically discuss the evidence and to take stock of our knowledge of AM fungi in agroecosystems, and perhaps to question cherished assumptions. However, we offer quite a different interpretation and conclusion, and propose a research track that envisages AM fungi – together with other soil biota – in an agricultural system that uses more sustainable analogs in terms of inputs and biodiversity. We cannot support the main conclusion captured in the title of Ryan & Graham (2018): 'Little evidence that farmers should consider abundance or diversity of arbuscular mycorrhizal fungi when managing crops'. We join Ryan & Graham (2018) in recommending that more critical research approaches and new methods are needed. These include better analytical tools (e.g. molecular methods, using mutants) and experimental designs (e.g. other response variables, including those that focus on long-term agricultural sustainability) to more precisely identify the various roles played by AM fungi in agricultural systems. We propose several high-priority research questions that should further such a research agenda (Table 1).

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