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Breeding for mycorrhizal symbiosis: focus on disease resistance

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Abstract Modern plant breeding can no longer afford to ignore the interaction between plants and microbial key players. Increasing evidence suggests (i) that the expression of many plant traits (such as nutrient use efficiency or tolerances against biotic and abiotic stresses) is mediated by beneficial microorganisms and (ii) that there is an exploitable genetic base for the regulation of symbiotic relationships. Arbuscular mycorrhizal fungi (AMF) play a key role in many of these trait expressions. While much is known about their ability to mobilise nutrients (especially phosphorus), the complex mechanisms of AMF-mediated disease resistance have only started to become apparent within the past decade. Besides competition for root space and resources, AMF also have the ability to induce plant defence mechanisms. Jasmonic acid (JA) and salicylic acid (SA) appear to be the key phytohormones that regulate relevant signalling pathways. The resulting activation of defence-related compounds can occur locally or systemically, constitutively or primed. Genotype-dependent plant reactions have been demonstrated for mycorrhizal responsiveness (when based on biomass), but not much is known when it comes to genotypic variation for AMF-mediated disease resistance. However, a few studies have provided first valuable insights. It is proposed to (i) include disease resistance as a factor to expand the term mycorrhizal responsiveness and (ii) make use of an indicator called "mycorrhiza use efficiency" as an additional measure to determine an optimum cost-benefit ratio of the mycorrhiza symbiosis. In order to detect differences in the efficiency, genotype selection needs to occur in environments that do not suppress the plant–microbe interaction. Thus, the value of organic breeding programmes is highlighted.

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Introduction

Many traits that breeders use as selection criteria are not mere plant but system traits involving the complex plant-associated microbial community (Berendsen et al. 2012; Philippot et al. 2013; Vandenkoornhuyse et al. 2015; Pieterse et al.

2016). Such system traits include nutrient use efficiency, drought and salt tolerance and disease resistance. When breeders select for these traits, they usually focus on their phenotypic expression without paying much attention to the role of associated microbes. However, it is well documented nowadays that microbes not only influence but are also part of that trait expression. For instance, the hyphal network of arbuscular mycorrhizal fungi (AMF) can access and mobilise plant unavailable phosphorus (P) and, as a result, improve the plant's P acquisition efficiency and, thus, increase the ability of the plant to use soil P in the production of biomass or yield (Sawers et al. 2010; Lehmann et al. 2012). Plants have the capacity to shape the composition and alter the activity of their associated microbes, e.g. via the exudation of flavonoids and other signalling compounds (Rengel 2002). If breeders were given tools to determine the influence of microbes on such system traits during the selection process, hidden capacities for the expression and also the stability of these traits could be revealed.

Arbuscular mycorrhizal fungi are of prime importance to most plants and are the best studied plant symbionts. Besides nutrient mobilisation (mainly phosphorus and zinc), benefits of mycorrhiza include improved tolerance against abiotic (mainly drought and salt) and biotic stresses (mainly soil-borne pathogens) (Azcón-Aguilar and Barea 1996; Parniske 2008). This mini-review will take the mycorrhiza symbiosis as a case study keeping in mind that many of the concepts mentioned here are also transferable to other symbiotic root endophytes such as rhizobia. We will summarise novel insights on a less known trait called AMF-mediated disease resistance and briefly explain the underlying mechanisms. With the demonstration of genotypic variation in mycorrhizal responsiveness (ability of the plant to respond to AMF) and first attempts to identify quantitative trait loci (QTL), we will bring the benefits of plant–microbe interactions (with a focus on improved disease resistance) into the context of plant breeding. We will highlight additional measures to improve the assessment of the AMF symbiosis and conclude with a perspective on how to make better use of plant–microbe interactions in breeding programmes.

Mycorrhiza-mediated disease resistance

Plants possess innate mechanisms to protect themselves against pathogens (Dangl and Jones 2001; Boller and He 2009; Thomma et al. 2011). At first, the plant recognises non-specific molecules such as flagellin, lipopolysaccharides or peptidoglycans, termed microbe-associated molecular patterns (MAMP, or PAMP in the case of pathogens). This recognition can activate responses in the host that lead to PAMP-triggered immunity (PTI). In return, pathogens can interfere with these responses by secreting effector proteins causing effector-triggered susceptibility (ETS). For instance, ETS has been demonstrated for pea. Pea plants reacted against *Fusarium solani* (Delserone et al. 1999) and *Didymella pinodes* (Yamada et al. 1989) with the accumulation of the phytoalexin pisatin. In both cases, the pathogen was shown to detoxify the phytoalexin, leading to a successful infection. In some cases, the plant can also recognise pathogen effectors and, in response, activate defence mechanisms that are quicker and stronger than those in PTI, resulting in effector-triggered immunity as shown for various Arabidopsis-pathogen systems (reviewed in Glazebrook 2005).

Plant defences can also be mediated by symbiotic root endophytes such as *Glomeromycota*, *Rhizobium*, *Trichoderma* or *Pseudomonas* spp. (Rhijn and Vanderleyden 1995; Harman et al. 2004; Parniske 2008; Raaijmakers et al. 2009; Gianinazzi et al. 2010). Plants benefit from root endophytes that extend their zone of activity beyond the rhizosphere (Feddermann et al. 2010; Hohmann et al. 2011, 2012). Arbuscular mycorrhizal fungi are such root endophytes that produce an extensive hyphal network. As one of the primary mutualistic plant–microbe symbioses, they have been shown to increase resistance against a wide range of fungal and bacterial pathogens (Azcón-Aguilar and Barea 1996; Whipps 2004). For instance, certain AMF such as *Funneliformis mosseae* (formerly known as *Glomus mosseae*) and *Rhizophagus irregularis* (formerly known as *G. intraradices*) were shown to alleviate symptoms of pea root rot caused by *Aphanomyces euteiches* (Bodker et al. 1998; Slezack et al. 1999) and *Pythium ultimum* (Merx 2004). Sikes (2010) reported that AMF species from the family *Glomeraceae* were effective at reducing *F. oxysporum* pathogen abundance in *Setaria glauca* while species from the *Gigasporaceae* were not. Recently, an

increasing number of studies have also reported mycorrhizal plants to be more resistant against foliar pathogens such as *Erysiphe pisi* in pea (Singh et al. 2002), *Magnaporthe oryzae* in rice (Campos-Soriano et al. 2012), *Alternaria solani* in tomato (Fritz et al. 2006; de la Noval et al. 2007) and *Botrytis cinerea* in roses and tomato (Møller et al. 2009; Pozo et al. 2010).

Higher tolerance against diseases (as well as increased plant growth and tolerance against abiotic stresses) were first exclusively attributed to an improved nutrient status (predominantly phosphorus) of the plant (Linderman 1994). More recent mineral supply experiments demonstrated that the beneficial effects cannot be solely explained by an improved nutrient uptake (Fritz et al. 2006; Liu et al. 2007). It became apparent that plants have the ability to regulate the AMF symbiosis. This autoregulative process was shown to prevent fungal pathogens from attacking roots (Vierheilig et al. 2008). In addition, AMF are able to directly reduce fungal infections, e.g., by competition for root space and resources (Azcón-Aguilar et al. 2002; Bødker et al. 2002; Harrier and Watson 2004; Wehner et al. 2010). An increasing number of studies also provide evidence of induced resistance mechanisms (Hause et al. 2007; Gutjahr and Paszkowski 2009; Jung et al. 2012). Mycorrhizal fungi initially trigger plant defence mechanisms similar to a biotrophic pathogen, but then modulate plant responses for a successful colonisation (Paszkowski 2006). Pozo and Azcón-Aguilar (2007) proposed that these modulations precondition the plant and, there-fore, efficiently activate plant defences upon pathogen attack. For instance, mycorrhizal plants showed enhanced levels of defence-related compounds, i.e. phenolics (López-Ráez et al. 2010a, b) and β-1,3-glucanase in tomato (Pozo et al. 1999), and chiti-nolytic enzymes in carrot (Benhamou et al. 1994) and pea (Slezack et al. 2000). Pozo et al. (1999) also showed evidence of priming reactions where different β-1,3-glucanase isoforms were upregulated in mycor-rhizal tomato plants only in the presence of the pathogen. However, not much is known about the systemic protection by AMF. A systemic upregulation of pathogenesis-related protein 1a and β-1,3-glu-canase was observed in the entire root system of partly mycorrhized tomato plants using split-root systems (Cordier et al. 1998; Pozo et al. 2002). In addition, Fiorilli et al. (2009) reported AMF-mediated changes in the expression of defence-related genes in

the shoots. Other studies mainly found transcriptional reprogramming of defence-related genes in roots (e.g. coding for chitinases, glucanases or phenylalanine ammonia-lyase) in tomato (Fiorilli et al. 2009; Lopez-Raez et al. 2010), rice (Campos-Soriano et al. 2012), and legume species including barrel medic (*Medicago truncatula*; Liu et al. 2007), soybean (Gao et al. 2012) and pea (Ruiz-Lozano et al. 1999).

Defence-related compounds are regulated by phytohormones (Pieterse et al. 2009). Salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) are key regulators of the defence mechanisms against pathogens. Salicylic acid is known to activate responses against biotrophic pathogens (Glazebrook 2005). It was also shown that AMF (being biotrophic) enhance levels of endogenous SA, but the initial increase is downregulated allowing the establishment of the symbiosis. Plant responses to necrotrophic pathogens are generally controlled by JA and ET pathways. Microbe-induced resistance is often regulated by the JA-pathway (Pozo et al. 2005; Van der Ent et al. 2009) and there have now been strong indications of JA to be involved in AMF-mediated resistance and priming (reviewed in Jung et al. 2012). Other phytohormones have been shown to regulate the formation of mycorrhizae. The full establishment of mycorrhizae is a prerequisite for symbiotic effects including mycorrhiza-mediated disease resistance (Slezack et al. 2000). For instance, a deficiency of abscisic acid (ABA) was shown to negatively influence mycorrhizal develop-ment and the functionality of arbuscules (Herrera-Medina et al. 2008; Garrido et al. 2010), possibly due to the upregulation of defence-related genes (Garrido et al. 2010). Strigolactones (SL) are recently identified phytohormones that stimulate spore germination and hyphal branching of AMF, but also trigger seed germination of parasitic plants (Gomez-Roldan et al. 2008; Foo and Reid 2012). Once mycorrhizae are established, SL levels are downregulated (Lendzemo et al. 2007; López-Ráez et al. 2011). Studies of an involvement of the phytohormone indole-acetic acid (IAA) have led to contradictory results (reviewed by Foo et al. 2013). For ectomycorrhizal fungi, Splivallo et al. (2009) found that IAA and ET play a key role as signal molecules in the fungus-plant interaction inducing alterations in root morphology. To some extent, there seems to be an indirect effect of IAA on

mycorrhizal formation by regulating SL levels (Foo et al. 2013).

In conclusion, it becomes apparent that AMF-mediated disease resistance is regulated both ways: AMF influence the defence mechanisms of the plant and the plant regulates the formation of mycorrhizae, which is a prerequisite for symbiotic effects. Further, defence responses can be upregulated locally in mycorrhizal roots or systemically within the entire plant and activated either constitutively or primed upon pathogen attack (Fig. 1). Discovering the balance of the SA and JA signalling pathways and their systemic regulation and regulatory effects on defence-related compounds will substantially improve our understanding of the AMF-plant interactions in general and AMF-mediated defence responses in particular.

Genotypic variation in mycorrhizal responsiveness

Plants have the ability to influence the microbial structure in the rhizosphere. It has been demonstrated that not only different plant species, but also different genotypes within the same species can modify the microbial community in the rhizosphere, e.g. by exudation of compounds that specifically stimulate or suppress particular pathogenic or beneficial microbes (Viebahn et al. 2005; Berg et al. 2006; Garbeva et al. 2007; Micallef et al. 2009; Aira et al. 2010; Doornbos et al. 2011; Peiffer et al. 2013). For instance, wheat cultivars have been found to differ in their ability to attract naturally occurring 2,4-diacetylphloroglucinol-producing *Pseudomonas* spp. (Gu and Mazzola 2003; Meyer et al. 2010). The amount of antibiotics produced by these biocontrol strains also differed
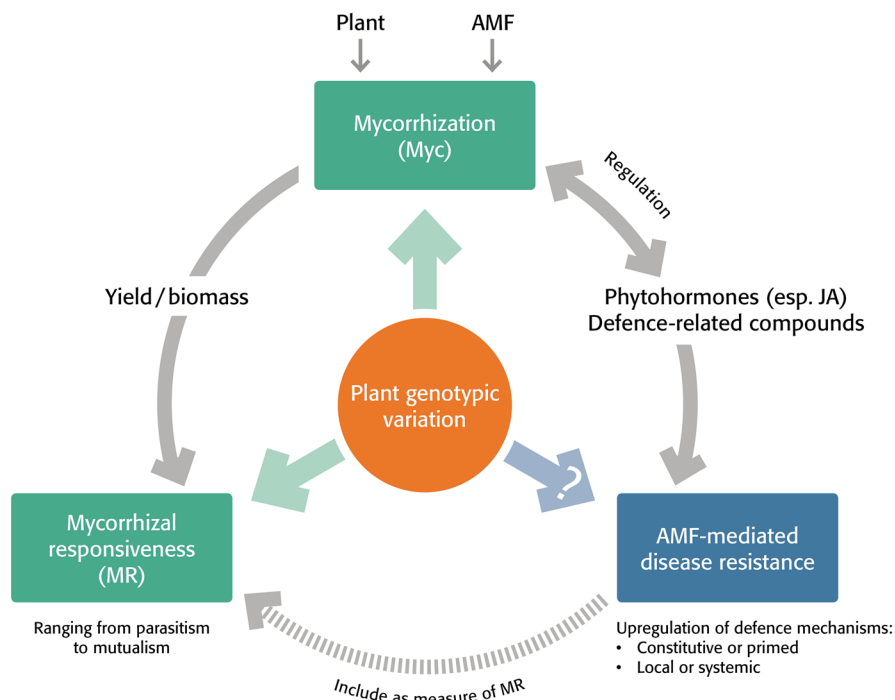
Fig. 1 A schematic illustration of the interaction between plants and arbuscular mycorrhizal fungi (AMF) with respect to AMF-mediated disease resistance. Two common ways to assess the plant-AMF interaction are mycorrhization (Myc; root colonisation and arbuscule formation) and mycorrhizal responsiveness (MR; ability of the plant to respond to AMF). Mycorrhization influences phytohormones, i.e. jasmonic acid (JA), and defence-related compounds. Both of which play a crucial role in AMF-mediated disease resistance that can be expressed constitutively or primed and locally or systemically. The plant in turn regulates the symbiosis via various phytohormone pathways. It is proposed to include AMF-mediated disease resistance as an additional measure of MR. Breeding can make use of the plant genotypic variation in mycorrhization and MR. However, the genotype-dependent plant reaction for AMF-mediated disease resistance needs further investigated

among the cultivars' rhizospheres. The ability of plants to respond to AMF can vary widely between plant species and among genotypes (Parke and Kaeppler 2000; Sawers et al. 2010). Genotypic differences in the response to AMF (based on biomass) have been observed in various crops, e.g., wheat cultivars (Hetrick et al. 1993), maize inbred lines (Kaeppler et al. 2000; An et al. 2009) and onion cultivars (Powell et al. 1982; Tawaraya et al. 2001; Galván et al. 2011). Such differences in mycorrhizal responsiveness (MR) indicate a genetic basis for the plant-AMF interaction. There have also been first attempts to identify QTL that govern MR for onion (Galván et al. 2011) and maize (Kaeppler et al. 2000).

Little is known about the genotypic variation in AMF-mediated disease resistance. Mark and Cassells (1996) showed a genotype-dependent interaction between the AM-fungus *Glomus fistulosum* and *Phytophthora fragariae* (the causal agent of red stele disease) in a population of outbreeding wild strawberry. Another study revealed cultivar-specific bioprotective effects by AMF when different tomato cultivars were infected with *Fusarium oxysporum* f. sp. *lycopersici* (Steinkellner et al. 2012). The mechanisms responsible for genotypic variation in AMF-mediated disease resistance are not yet understood and need further investigation in order to fully exploit the benefits of this particular plant–microbe interaction. Promising results were shown in other systems. For instance, Smith and Goodman (1999) were able to identify three QTL associated with disease suppression of *Pythium torulosum* in tomato by the rhizobacterium *Bacillus cereus* explaining 38% of the phenotypic variation. Worth mentioning here is also a pioneering study by Horton et al. (2014) who looked at the microbial community as a whole. They discovered QTL that govern the microbiome composition of endophytic bacteria in *Arabidopsis thaliana*. The above mentioned studies (and also findings from previously mentioned studies such as Hetrick et al. 1993; Kaeppler et al. 2000; Powell et al. 1982; Tawaraya et al. 2001) indicate that modern plant breeding may have selected against plant traits essential for hosting and supporting beneficial microbes. However, they also indicate the presence of genetic variation that can be exploited to enhance beneficial interactions between plants and AMF and other members of the microbial community.

Exploit the mycorrhizal symbiosis in plant breeding

The extent in which mycorrhizal strains provide benefit to the plant can range from mutualistic to parasitic effects (Klironomos 2003). In turn, plants have the ability to differentially allocate resources to beneficial symbionts (Kiers et al. 2003; Bever et al. 2009). It is assumed that plants show variation in their efficiency to regulate the symbiosis. When screening 104 pea genotypes for their ability to interact with the AM-fungus *R. irregularis*, mycorrhizal responsiveness (MR; expressed as the difference in shoot dry weight between mycorrhized and non-mycorrhized plants) and mycorrhization (expressed as % root length colonised (RLC) by arbuscules) ranged widely among those genotypes (Hohmann et al. 2016). However, there was no significant correlation between MR and mycorrhization (Fig. 2). The absence of a positive correlation between mycorrhization and MR (based on biomass, shoot P or grain yield) was also shown in several other studies (Krishna et al. 1985; Baon et al. 1993; Kaeppler et al. 2000; Alvey et al. 2001; Ryan et al. 2002; Ryan and Angus 2003; Hildermann et al. 2010; Smith and Smith 2012; Leiser et al. 2016). Leiser et al. (2016) concluded that there is no need to breed for enhanced AMF root colonisation
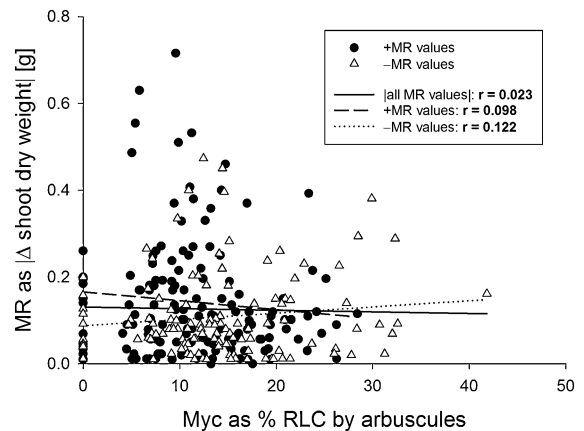
Fig. 2 Scatter plot between mycorrhizal responsiveness (MR; expressed as absolute difference in shoot dry weight between mycorrhized and non-mycorrhized plants) and mycorrhization (Myc; expressed as percentage root length colonised (RLC) by arbuscules) assessing 104 pea genotypes (data from Hohmann et al. 2016). *Filled circles* and *open triangles* show positive and negative MR values, respectively. The *solid*, *dashed* and *dotted lines* indicate linear regression between % RLC and absolute, positive and negative MR values, respectively

to improve low-P adaptation. The authors agree that mere selection for high AMF root colonisation might not be sufficient. Even the selection for MR can lead to biased or inconclusive results. Sawers et al. (2010) discussed the issue in detail and presented an approach to identify genotypes with high MR while eliminating performance variation of non-mycorrhized plants using P dose–response experiments.

We propose an additional measure to estimate the efficiency of the plant-AMF interaction since mycorrhization and MR on their own might not indicate an optimum cost-benefit ratio of this symbiosis. A term called mycorrhiza use efficiency (MUE) gives an indication of the benefit per mycorrhizal unit. Mycorrhizal use efficiency can be defined as:

$$MUE = MR\ /\ Myc$$

dividing mycorrhizal responsiveness (MR) by any form of quantification of mycorrhization (Myc; e.g. % root length colonised (RLC) or AMF-specific DNA copy number). Applying this to the data mentioned in Fig. 2, MUE differs significantly among the pea genotypes ranging from −61 to +159 mg shoot dry weight difference between mycorrhized and non-mycorrhized plants/% RLC by arbuscules (Fig. 3).

Any indicator to describe the mycorrhiza symbiosis that has been discussed in the past decades has their own advantages and disadvantages. While the two main advantages of MUE are its simplicity and possibility to determine how efficiently each mycorrhizal unit contributes to MR, some issues with MUE need also to be mentioned. First, MUE is biased towards low colonisation rates resulting in abnormally high MUE values. It is therefore necessary to choose a lower boundary and exclude plants that fall below this boundary level. Second, using MR in the calculation of MUE still includes variation linked to differences in plant performance in non-mycorrhized plants. In addition, we still do not know how mycorrhization or MR (when based on biomass or yield) affect other important traits elicited by AMF (e.g. disease resistance, phosphorus use efficiency (PUE) or drought tolerance). Therefore, instead of using MR, MUE could also be based on relevant dose–response indicators (e.g. the positions of the inflection points; see Sawers et al. 2010) or other important traits such as disease resistance. In fact, there are indications that the efficiency of AMF-mediated disease resistance might also be subject to variation. For instance, in the
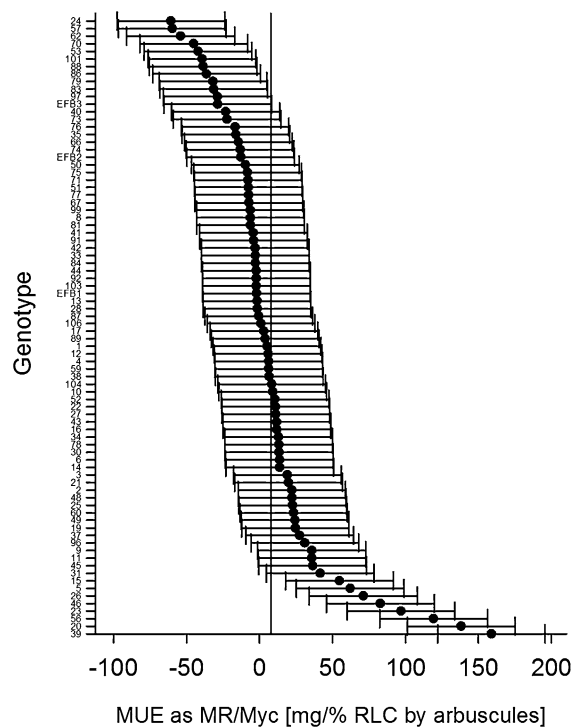
Fig. 3 Mycorrhizal use efficiency (ME; expressed as the quotient between mycorrhizal responsiveness (MR; see Fig. 1) and mycorrhization (Myc; see Fig. 1)) for 82 pea genotypes (data from Hohmann et al. 2016). Values shown are the means (n = 4) and bars represent Tukey 95% confidence intervals for all pairwise comparisons. The *solid vertical line* shows the overall ME mean. Genotypes with mycorrhization <2% RLC are excluded

previously discussed study of Mark and Cassells (1996), there was a plant genotype-dependent mediation of disease resistance by *G. fistulosum* with no apparent relationship between mycorrhizal root colonisation and AMF-mediated disease resistance.

In order to make use of MUE (or any other symbiosis indicator for that matter), it is essential to select in environments that favour the interaction between plants and AMF (reviewed Bennett et al. 2013). Organic farming systems are known to provide more favourable conditions for mycorrhiza compared with conventional farming (Hildermann et al. 2010) that usually applies fungicides and relatively high and easily available amounts of P. It was shown that organic farming systems accommodate higher AMF spore abundance and species diversity, and result in increased AMF colonisation rates and a compositional structure that is more similar to natural ecosystems (Mäder et al. 2000; Oehl et al. 2004; Galván et al.

2009). Commonly used fungicides (foliar applications as well as seed treatments) can detrimentally affect AMF spore germination, mycorrhiza formation, AMF community composition, extra-radical hyphae and/or spore production (Dodd and Jeffries 1989; Merryweather and Fitter 1996; Hernández-Dorrego and Mestre-Parés 2010; Jin et al. 2013; Buysens et al. 2015). Available soil P correlates negatively with mycorrhization and MR and, thus, affects P mobilisation by AMF (reviewed by Morgan et al. 2005). Breeding under high P conditions might therefore indirectly select for poor AMF hosts (Wissuwa et al. 2009; Lehmann et al. 2012; Bennett et al. 2013). We hypothesise that a reduced mycorrhizal dependency also affects other benefits elicited by AMF such as disease resistance. We therefore pledge to include factors other than biomass to estimate MR and MUE, i.e. disease resistance (but also PUE or drought tolerance) to obtain a comprehensive differentiation of the plant-AMF interaction. In conclusion, the selection process will have to occur under conditions (e.g. organic) that do not suppress the establishment and, thus, beneficial effects of this symbiosis, in order to identify plant genotypes that make efficient use of the soil AMF community in arable production systems.

Conclusions

The genetic base for the regulation of the symbiosis leading to opportunities for human-imposed selection to extend and improve benefits by AMF has become more and more evident. Nowadays, with the availability of genome-wide marker coverage available for many crop species (incl. important leguminous crops), we will be able to increase the explained variance of QTL that govern plant traits such as disease resistance, and, consequently, develop improved marker-assisted selection tools for those traits. Phosphorus mobilisation is not the only important mode of action of the mycorrhiza symbiosis. Besides the need for organic (or low input) breeding programmes to fully exploit AMF-mediated plant traits, it remains crucial to better understand the heritability of those system traits. The authors pledge to extend the term MR to include other important traits such as disease resistance and include mycorrhizal use efficiency as an additional measure to help establish an efficient balance between plants and

AMF for optimised yield and yield stability. Finally yet importantly, some of the above-mentioned concepts can also be applied to the plant-associated microbial community as a whole. The analysis of genotypic variation in microbiome composition and functioning will help to identify microbial hubs and key pathogens and beneficials that play a crucial role in the expression of system traits. This will provide crucial information towards the development of novel breeding tools to make efficient use of plant–microbe interactions during the selection process.

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