Chapter 3

Benefits of Breeding Crops for Yield Response to Soil Organisms

ALISON E. BENNETT, TIMOTHY J. DANIEL, and PHILIP J. WHITE
The James Hutton Institute, UK

3.1 INTRODUCTION

The Agrarian Revolution is considered to have begun approximately 10,000 years ago and is associated with the transition of human communities from hunting and gathering to settlement and agriculture (Fig. 3.1). Over the millennia since then, the domestication of wild species, the selective breeding of high yielding genotypes, and numerous technological advances have enabled the production of edible crops to increase and thus support the nutritional requirements of a global population of over 7 billion people (FAO, 2012). In the recent past, during the period known as the Green Revolution (1950–present), crop production increased dramatically (Fig. 3.1; FAO, 2012). This was founded mainly on the development of semi-dwarf cereal crops and crops resistant to pests and pathogens, whose yields are maintained through the application of agrochemicals to control weeds, pests, and diseases, mineral fertilizers, and irrigation (Evans, 1997; Godfray et al., 2010; Fageria et al., 2011; White et al., 2012). In recent decades, the consumption of natural resources to deliver fertilizers, agrochemicals, and clean water to agriculture, and to build and maintain the infrastructures required for crop production has accelerated (Fig. 3.1; FAO, 2012). This has incurred increasing economic and environmental costs (Nellemann et al., 2009; Rockström et al., 2009; Vitousek et al., 2009; White and Brown, 2010; Dawson and Hilton, 2011). It is now evident that if agriculture is to support the human populations predicted for the next decades through the millennia ahead, more sustainable strategies for crop production must be developed (Graham et al., 2007; White and Brown, 2010).

It is hoped that the beneficial relationships between crop plants and their symbionts, and their combined influence on the biology, chemistry, and physics of the rhizosphere and soil can be exploited for this sustainable intensification of crop production (Graham et al., 2007; Fageria et al., 2011) to create a new revolution in crop production, which is referred to as the Evergreen Revolution (Fig. 3.1).

Plants, agricultural and otherwise, associate with a wide variety of soil organisms. These associations are often ignored because they are not easily visible, yet soil organisms can influence the phytoavailability and uptake of water and essential mineral elements by plants, which in turn can influence plant growth and crop yield (Morgan et al., 2005). Modern agricultural practices have, for the most part, eliminated the dependence on soil organisms by providing plant nutrients, pathogen defense, and herbivore defense with inputs of mineral fertilizers and agrochemicals. However, as peak oil and peak phosphorus begin to limit the availability of inorganic fertilizers and synthetic agrochemicals (Raven, 2008; Cordell et al., 2009; Dawson and Hilton, 2011), agriculture will need to employ more sustainable means of crop production.

The future sustainability of agricultural production will depend more upon utilizing positive associations with soil organisms while avoiding negative associations. For example, a wide variety of different soil organisms can increase the phytoavailability of essential mineral nutrients. Mutualists such as mycorrhizal fungi and rhizobia can acquire essential mineral elements that often restrict crop production, such as phosphorus (P) and nitrogen (N), and deliver them directly to their host plants, whereas free-living organisms such as those involved in...
18 Chapter 3 Benefits of Breeding Crops for Yield Response to Soil Organisms

Mycorrhizal response
Loss to pathogens
Agricultural natural N fixation
Agricultural revolution
Land race selection
Heritage varieties
Modern varieties
Responsive varieties?

Figure 3.1 (a) Schematic representations of global human population (black line), global cereal production (red line), global consumption of N-fertilizers (green line), P-fertilizers (blue line), and agrochemicals (purple line) during the Agrarian Revolution and the Green Revolution (1950–2010) and their projections for the future based on business-as-usual (dotted lines) or the adoption of more sustainable practices (Evergreen Revolution; dashed line). (b) Schematic representations of “boom-and-bust” cycles in crop losses to pathogens (purple line), response of crop yield to AM-fungi (blue line), and biological nitrogen fixation in agriculture (green line).

Plants can associate with soil organisms with both positive and negative effects and it is the net effect of these associations that will ultimately determine crop yield. To date, it has remained impossible to dissect the complex interactions among soil communities that result in variations in crop yields. However, a common method to assess the magnitude of these interactions is to determine the response of the system to perturbation. The term “response” was first coined to describe the influence of arbuscular mycorrhizal (AM) fungi on plant growth among multiple plant species (Plenchette et al., 1983; Hetrick et al., 1990). However, this variable has been expanded to describe the influence of a wide variety of soil organisms, either individually or collectively, on plant growth and crop yields (e.g., Vandeguchte et al., 2010; Bennett et al., 2011). There are several different metrics for response (Righetti et al., 2007), but all measure the variation between growth in the presence or absence of a test organism.

In this chapter we focus on the response of plants to three commonly studied groups of soil organisms (pathogens, AM fungi, and rhizobia) that have the potential to exert strong influences on crop production. We describe the interactions between these organisms and crop plants, and their potential influence on crop yields. We also examine how breeding might have influenced the responses of crop plants to these organisms to provide insight to the potential of using these organisms to improve crop production with reduced agricultural inputs.

The first group of soil organisms we consider is soil pathogens. These attack crop species and result in reduced crop yields. Extensive efforts have been made to breed crops for resistance to soil pathogens. When resistant genotypes are not available, soil pathogens can be controlled by agronomic practices such as the application of agrochemicals (fungicides, pesticides, insecticides), soil ameliorants to modify soil pH, fertilizers to maintain plant vigor, or irrigation, as in the case of common scab of potatoes.

The second group of soil organisms we consider is AM fungi, which can supply essential mineral elements...
with restricted phytoavailability, such as P and micronutrients, to the host plant in exchange for carbon (Morgan et al., 2005; Smith and Read, 2008; see Chapter 43). As a result, AM fungi could play a big role in the P nutrition of plants, and in P cycling within agricultural fields, thereby contributing to sustainable crop P nutrition. In addition, AM fungi have been shown to improve plant water uptake (Smith and Read, 2008), reduce the impact of pathogens (Borowicz, 2001; Pozo and Azcon-Aguilar, 2007), and alter plant secondary chemistry (Gange and West, 1994; Bennett et al., 2009). Despite the many potential benefits of AM fungi, the actual outcome of an association with a host plant depends greatly on specific interactions with different AM fungal species and the phytoavailability of phosphorus (Smith and Read, 2008).

The third group of soil organisms we consider are nitrogen-fixing bacteria (such as rhizobia, bradyrhizobia, and azorhizobia), which are commonly utilized to supplement N-fertilizer additions in agriculture (Fageria et al., 2011; White et al., 2012; see Section 6). These bacteria inhabit nodules that form in the roots or the stems of legume species, and fix atmospheric nitrogen for their plant hosts. The N fixed by rhizobia can increase N supply not only to the host legume but also to the intercropped plants and to the subsequent crops in rotations. The utilization of nitrogen-fixing bacteria should reduce the requirement for N-fertilizers in agriculture, although there will still be an absolute requirement for chemical inputs to maintain sufficient crop production for the world’s human population, if it follows current trajectories (Graham et al., 2007; Erisman et al., 2008; Dawson and Hilton, 2011; Fig. 3.1). Today, it is estimated that biological nitrogen-fixation inputs 50–70 Tg N annual to agricultural systems (Herridge et al., 2008), which compares to approximately 100 Tg N per year produced through the Haber–Bosch process and applied as inorganic N-fertilizer (Fig. 3.1; Gruber and Galloway, 2008).

3.2 Has Breeding Reduced The Yield Response of Crops to pathogens?

Potential losses due to pathogens have been estimated to be about 9–21% of global crop production (Oerke, 2006), but global losses due to specific root pathogens have rarely been estimated. Pathogens have the greatest effect in monoculture systems when adaptation to overcome resistance in a common crop genotype can have catastrophic effects, as illustrated by the Great Irish Potato Famine (Lucas, 1998).

Before monocultures of a single crop genotype became popular it is assumed that instances of catastrophic losses in crop productivity resulting from the overabundance of a particular pathogen were rarer, less intense, and likely driven by local dynamics (Fig. 3.1). The severity and frequency of individual outbreaks of disease, root and otherwise, likely increased due to the introduction of monocultures, resulting in regular “boom-and-bust” yield cycles linked to breeding cycles. In these cycles, breeders discover genetic resistance to a pathogen (or pathogen strain), introduce a resistant genotype leading to increased crop productivity, then a pathogen capable of overcoming crop resistance evolves, which results in renewed crop losses. For example, the Great Irish Potato Famine of the 1850s led to a wide search for genotypes and species of potato resistant to Phytophthora infestans, the cause of the famine (Lucas, 1998). Researchers eventually developed resistant genotypes by creating hybrids between the common potato, Solanum tuberosum, and wild relatives such as Solanum demissum and Solanum berthaultii (Lucas, 1998). The initial resistant varieties were grown widely until their resistance was overcome by another strain of P. infestans leading to renewed crop losses. The cycle of selection for genotypes of cultivated potato with resistance to P. infestans and the subsequent evolution of P. infestans to overcome crop resistance continues today.

During the Green Revolution, farmers began combining the cultivation of crop genotypes with resistance to pathogens with an increased use of agrochemicals to reduce losses from pests and diseases (Fig. 3.1). Today, root pathogens are still controlled through this two-pronged approach: application of fungicides and breeding for resistance. Modern breeding for resistance to root pathogens takes a more active role than merely selection and mating of resistant and susceptible genotypes. Molecular tools have grown in use, and the use of irradiation, cell culture, and direct genetic manipulation have all been used to breed crop genotypes resistant to P. infestans and the subsequent evolution of P. infestans to overcome crop resistance continues today.

In these cycles, breeders discover genetic resistance to a pathogen (or pathogen strain), introduce a resistant genotype leading to increased crop productivity, then a pathogen capable of overcoming crop resistance evolves, which results in renewed crop losses. For example, the Great Irish Potato Famine of the 1850s led to a wide search for genotypes and species of potato resistant to Phytophthora infestans, the cause of the famine (Lucas, 1998). Researchers eventually developed resistant genotypes by creating hybrids between the common potato, Solanum tuberosum, and wild relatives such as Solanum demissum and Solanum berthaultii (Lucas, 1998). The initial resistant varieties were grown widely until their resistance was overcome by another strain of P. infestans leading to renewed crop losses. The cycle of selection for genotypes of cultivated potato with resistance to P. infestans and the subsequent evolution of P. infestans to overcome crop resistance continues today.
for the likely reduction in agrochemical inputs, we might expect to see more frequent and catastrophic crop losses (Fig. 3.1).

3.3 HAS BREEDING REDUCED THE YIELD RESPONSE OF CROPS TO AM FUNGI?

3.3.1 Genetic Variation in Response to AM Fungi among Crop Species

Unlike the situation for pathogens, there has not been any directed breeding effort to influence interactions between plants and AM fungi. As a result, there is very little historical literature investigating changes in the response of crop plants to AM fungi. Indeed, the study of AM fungi has a relatively short history of about 100 years (Smith and Read, 2008), which is significantly shorter than the length of time that pathogens have been observed and studied (centuries). However, it seems likely that breeding efforts, particularly modern breeding efforts, have selected for crop plants with a reduced response to AM fungi—a trait that may pose problems in the future if the availability of P fertilizers becomes limiting.

In order for breeding to select for a reduced response to AM fungi, there must be genetic variation within crop species for this trait. To our knowledge, response to AM fungi has not been tested directly in the founder populations of any crop species. However, variation in response to AM fungi has been demonstrated among genotypes of cultivated crops and in natural populations of species in a number of different ways. For example, variation in response to AM fungi has been reported among near isogenic lines derived from four Trifolium repens parents (Eason et al., 2001) and among genotypes of several Medicago spp. (Monzon and Azcon, 1996). Variation in response to AM fungi has also been found between introduced and native genotypes of Hypericum perforatum (Seifert et al., 2009), suggesting that selective pressures can act on introduced species in their new range to alter their response to AM fungi. Similarly, the invasive grass Holcus lanatus was shown to have a smaller response to AM fungi despite a higher level of AM fungal colonization than the native plant Eragrostis glauca in a Californian coastal prairie (Bennett et al., 2011). Studies of H. lanatus in its native European habitat revealed a different pattern in which H. lanatus responds positively to AM fungi and its soil community (Bischoff et al., 2006; Macel et al., 2007). This supports the hypothesis that introduced plant species can experience selective pressures that reduce their response to AM fungi. Finally, it has been demonstrated in six Plantago lanceolata genotypes that variation in response to a single AM fungal species is correlated with response to any other AM fungal species regardless of the total benefit provided by the AM fungal–plant combination (Fig. 3.2). There was variation in the response of P. lanceolata genotypes to different fungal species, but plant genotypes that attained the highest biomass with one fungal species also attained the highest biomass with every other species. This result suggests that plant response to one community of AM fungi is correlated with plant response to any other AM fungal community. While all these studies were conducted in greenhouse settings, analogous results have been obtained under field conditions (Pringle and Bever, 2008). We therefore conclude that (i) variation in natural plant populations for responsiveness to AM fungi exists, (ii) selection on responsiveness to AM fungi can occur, and (iii) selection in host plants in response to one AM fungal community will likely influence response to other AM fungal communities.

Although the founder populations of crop plants have, to our knowledge, never been tested for their response to AM fungi, we can base predictions about the propensity for variation in response to AM fungi in particular crop species on phylogenetic comparisons (Fig. 3.3). Wilson and Hartnett (1998) examined 99 plant species from a prairie habitat and observed great variation in their response to AM fungi. These plant species and their response to AM fungi can be placed on a phylogenetic tree along with the 21 most important crop species (Fig. 3.3). From this analysis, the response to AM fungi of particular plant species can be predicted. For example, it can be observed that grasses from the
3.3 Has Breeding Reduced The Yield Response of Crops to AM Fungi?

![Phylogenetic distribution of mycorrhizal responsiveness (%) among the angiosperm families surveyed by Wilson and Hartnett (1998). Values are means of data for the number of species (n) surveyed in each plant family, with the exception of values for the Poaceae, which are means of data for the number of species (n) surveyed in each tribe. The phylogenetic position of the 21 most important crops based on world production figures for 2010 (FAO, 2012) are also indicated. The phylogenetic tree is based on that of The Angiosperm Phylogeny Group III (2009).](image)

subfamily Pooideae (tribes Aveneae, Bromeae, Poeae, and Triticeae) tend to have a low response to AM fungi. This observation is consistent with many independent studies. Nevertheless, even in species from these clades, genetic variation in response to AM fungi has been reported. For example, variation in response to AM fungi has been shown repeatedly among wheat genotypes (Jun and Allen, 1991; Hetrick et al., 1992, 1993, 1996; Yao et al., 2001a, 2001b), although older wheat cultivars have been shown to have a greater response to AM fungi than recent cultivars (Kapulnik and Kushnir, 1991; Zhu et al., 2003). Variation among genotypes in response to AM fungi has also been demonstrated in barley (Zhu et al., 2003) and pearl millet (Krishna et al., 1985).

To add further weight to assertion that responsiveness to AM fungi is a genetic trait and can be selected upon, wheat genes responding to colonization by AM fungi have been identified on chromosomes 5 and 7 in the B and D genomic backgrounds (Hetrick et al., 1995).

In contrast to the grasses discussed earlier, grasses from the Chloridoideae subfamily (tribes Cynodonae, Eragrostideae, and Zoysiaeae) and the Panicoideae subfamily (tribes Andropogonodae and Panicaeae) tend to respond strongly to AM fungi (Fig. 3.3). This has been confirmed in several studies of maize genotypes (Khalil et al., 1994; Al Karaki and Al Raddad, 1997; Kaeppler et al., 2000; Karasawa et al., 2001; Karasawa et al., 2006; Reis et al., 2006). In addition, significant variation in root colonization by AM fungi has been demonstrated among 100 maize genotypes, with variation being greatest among land races and hybrids (An et al., 2010). These observations suggest that there is inherent genetic variation across the breeding history of maize for association with, and potential response to, AM fungi. Variation in response to AM fungi among
genotypes has also been demonstrated in sorghum, a member of the Andropogonodae (Mehran et al., 2009). This research supports the notion that there is genetic variation in response to AM fungi among cereal cultivars derived from founder Poaceae populations that can be selected upon to improve yield response to AM fungi. The majority of research on the responses of crop species to AM fungi has been conducted on cereal crops. However, there is also much research documenting variation in the response to AM fungi among genotypes of other major plant families and crop species. For example, within the Fabaceae there is a great range of response to AM fungi. This family contains species that respond strongly to AM fungi as well as the non-responding species (Wilson and Hartnett, 1998), resulting in a predicted medium level of response for the family as a whole (Fig. 3.3). Variation in response to AM fungi among genotypes of several crop species in the Fabaceae has been documented. These species include chickpea (Cicer arietinum; El Ghandour et al., 1996; Konde and Deshmukh, 1996), lentil (Lens culinaris; Krishnareddy and Ahlawat, 1996), groundnut/peanut (Arachis hypogaea; Daft, 1991; Ibrahim et al., 1995), and soybean (Glycine max; Khalil et al., 1994). Although there are few agricultural species in the Asteraceae, and none in the list of 21 most important crops (FAO, 2012), this family contains many horticultural species. From the data of Wilson and Hartnett (1998), this family is predicted to have a medium level of response to AM fungi (Fig. 3.3). Studies of a horticultural species, marigold (Tagetes spp.), have supported the prediction of responsiveness to AM fungi and also demonstrated variation among genotypes (Linderman and Davis, 2001). Although the study by Wilson and Hartnett (1998) investigated the AM responsiveness in a great number of different families and phylogenetic groupings, it did not include all of the phylogenetic groupings we might consider important for agriculture (Fig. 3.3). For example, no species from the Solanaceae were contained in the survey. However, there have been several studies on the response to AM fungi of crop species of the Solanaceae that have shown variation among genotypes including studies on tomato (Solanum lycopersicum; Bryla and Koide, 1998, Al Karaki et al., 2001), Solanum aethiopicum (a crop grown in Africa) (Diop et al., 2003), and pepper (Capsicum annuum; Sensory et al., 2007). The Rutaceae genotypes from several citrus species have shown variation in their response to AM fungi (Graham et al., 1997). Unfortunately, not all plant families were well represented in the study of Wilson and Hartnett (1998). For example, only one member of the Rosaceae was tested and it was reported to respond negatively to AM fungi. However, strawberry, also a member of the Rosaceae, generally responds strongly to AM fungi, but also varies in the magnitude of its response (Vestberg, 1992). For several of the less commonly cultivated plant species, it is difficult to make predictions about their responsiveness to AM fungi. However, genotypes of sesame (Sesamum indicum; Sulochana et al., 1989), acerola (Malpighia emarginata; Costa et al., 2001), mulberry (Morus spp.; Venkataramana et al., 2007), grapevine (Vitis vinifera; Linderman and Davis, 2001), and papaya (Carica papaya; Trindade et al., 2001) all vary in their response to AM fungi. Thus, we can conclude that (i) variation in response to AM fungi is a widespread trait likely to occur in all cultivated crop species, (ii) the potential magnitude of responsiveness of a particular species can be predicted by knowledge of the responsiveness of wild or cultivated relatives, and (iii) variation in response to AM fungi is a genetic trait that can be selected upon.

### 3.3.2 Breeding for Response to AM Fungi in Crop Species

Response to AM fungi is not a trait for which breeders have intentionally selected when developing new varieties. Instead, any selection on response to AM fungi by crop species has been unintentional and due to undirected selection pressures. Researchers studying AM fungi generally agree on three undirected selection pressures in the breeding process that disturb the AM fungal–plant mutualism, and could result in selection for reduced response to AM fungi: soil disturbance, high nutrient availability, and monoculture.

The AM fungal hyphal network in soil acquires nutrients for host plants, transfers carbon between hosts, and, in some species, eliminates their ability to colonize new host plants. As a result, plants grown in tilled soils are less likely to encounter AM fungi than plants grown in undisturbed environments, and lack of AM fungal associations, in particular with a diversity of AM fungi, might limit plant growth and crop yields.

When the phytoavailability of mineral nutrients, especially P, is high, AM fungi still colonize host plant roots, but no longer provide a benefit. Instead, they become a carbon drain on their host and are considered to be parasitic (Smith and Read, 2008). Thus, in well-fertilized agricultural systems, plant genotypes that can limit their association with AM fungi are likely to perform best. High
3.4 Has Breeding Reduced The Yield Response of Crops to Rhizobia?

To our knowledge, variation in the response of founder populations of legume crops to rhizobial colonization has not been estimated. However, variation in response to rhizobia (Yates et al., 2011) has been demonstrated in natural populations of legume species (e.g., Elliott et al., 2009) and there have been many studies describing variation in response to rhizobia among cultivars and genotypes of particular legume species (e.g., Chaverra and Graham, 1992; Abi-Ghanem et al., 2011; Biabani et al., 2011). These studies have identified various characteristics that are correlated with increased nitrogen fixation. For example, in common bean (Phaseolus vulgaris) variation in nitrogen fixation has been associated with early nodulation, for which there is considerable genetic variation (Chaverra and Graham, 1992), and with the size of root nodules (Paula Rodino et al., 2011), and in peas and lentils increased nitrogen fixation is correlated with nodule number (Abi-Ghanem et al., 2011). Differences in such characteristics can lead to considerable variation in nitrogen-fixing capability among cultivars of legume crops.

There have been fewer comparisons of the response to rhizobia of wild and bred genotypes of particular legume species. As a result, although there are suggestions of reduced rhizobial association, and reduced nitrogen fixation, among cultivated legumes, for example, in chickpea (Biabani et al., 2011), further evidence needs to be collected. It appears that many of the same selective pressures influencing crop response to AM fungi, such as increased soil disturbance, high phytoavailability of nutrients and monoculture, are likely to act as selection pressures in the legume–rhizobia system. As rhizobia can live freely in the soil without a host, the effects of tillage are likely to be less severe for the legume–rhizobia association than for the AM fungal–plant association. However, soil disturbance, particularly burying of rhizobial cells deeper in the soil during tillage, likely reduces encounters between host plants and bacterial partners, thereby reducing the period of symbiotic nitrogen fixation in an annual crop.
Intensive agriculture with high N-fertilizer inputs reduces the dependence of legumes on biological nitrogen fixation. In addition, studies have shown that greater N-phytoavailability reduces the efficacy of the legume–rhizobia symbiosis by reducing overall nodulation as well as the level of nitrogen fixation per nodule (e.g., Hungria et al., 2006). When N-fertilizer inputs are high, genotypes with reduced rhizobial associations are likely to have higher yields because they receive sufficient N and do not deliver C to rhizobia. Thus, selecting for increased yield in agricultural systems with high N-fertilizer inputs would inadvertently select for reduced rhizobial associations.

The response of rhizobia to monocultures is unknown, but it is known that multiple genotypes of rhizobia can associate with a specific host plant. Crop species grown repeatedly in monoculture tend to have a greater specificity for particular rhizobial strains than nonagricultural species growing in more diverse plant communities (Provorov and Tikhonovich, 2003; Mutch and Young, 2004). This suggests that legume genotypes bred for improved yields when grown in monoculture are less able to support a diverse community of rhizobia, which might influence the efficacy of subsequent symbiotic nitrogen fixation in arable fields.

Very clearly breeding and cultivation of legumes in systems with high N-fertilizer inputs has influenced legume–rhizobia associations. Selection has acted on traits associated with biological nitrogen fixation, such as early nodulation (Chaverra and Graham, 1992), nodule number (Abi-Ghanem et al., 2011), and nodule biomass (Paula Rodino et al., 2011), but genetic variation in these characteristics still persists. Breeding has resulted in legume genotypes with a higher specificity for rhizobial symbionts, which are then less able to associate with the wider population of rhizobial strains found in nature (Provorov and Tikhonovich, 2003; Mutch and Young, 2004). Thus, it is not surprising that researchers have been calling for breeding programs to focus on biological nitrogen fixation in legumes (Ranalli and Cubero, 1997; Herridge et al., 2008; Biabani et al., 2011), and identifying breeding strategies for increasing biological nitrogen fixation in agriculture (Barron et al., 1999).

Given the large genetic variation in response to rhizobia within many legume species, the question arises: Can breeding strategies be developed to increase biological nitrogen fixation under field conditions and, thereby, reduce our dependence on the Haber–Bosch process and synthetic N-fertilizers? The answer to this question is unequivocally: Yes. This approach has been led by Latin American countries, particularly Brazil and Australia, who have created legume-breeding programs that target increasing nitrogen fixation in legumes directly (Nicolas et al., 2002; Alves et al., 2003; Hungria et al., 2005; Unkovich et al., 2008) and also investigate the management of external factors, such as the appropriate use of rhizobial species for each soil type, to maximize the benefit of biological nitrogen fixation to crop production (Hungria and Vargas, 2000). These breeding programs have been quite successful, and have reduced the need for N-fertilizer additions. As a result, breeding for increased nitrogen fixation in leguminous species, with its application in both intercropping and rotations, appears to be a viable and sustainable strategy for reducing our dependence on synthetic N-fertilizers.

### 3.5 Conclusion

This chapter has described how breeding has influenced crop responses to pathogens, AM fungi, and rhizobia. It has been observed that conventional breeding efforts appear to have selected for reduced responses to all three groups of soil organisms, whether intentionally or unintentionally. Most people would agree that reduced responses to pathogens provide a benefit, whereas reduced responses to AM fungi and rhizobia, although having little effect under current practices in intensive agriculture involving tillage, fertilizer additions, and monoculture, might restrict future crop production should the availability of mineral fertilizers become limiting, or policy and environmental pressures, such as the need for increased carbon storage in soils, alter tillage practices.

In the future, it is likely that sustainable mineral nutrition of crops will require beneficial relationships with soil organisms such as AM fungi and rhizobia, and this will ultimately influence breeding strategies. The major challenge for breeders will be to reduce the detrimental effects of pathogens while increasing associations with beneficial organisms such as AM fungi and rhizobia. Superficially, this process seems simple enough. Breeders might develop genotypes resistant to pathogens with relatively high levels of association with AM fungi and rhizobia. However, AM fungi and rhizobia both trigger and then shut down the salicylic acid pathway, which is a key determinant of their host plant’s response to pathogen infection. These effects on the salicylic acid pathway could have various consequences. For example, genotypes bred for a reduced response to pathogens might also have reduced associations with AM fungi and rhizobia (Toth et al., 1990) or colonization by AM fungi and rhizobia might prime plants for faster responses to pathogens. Although we know of no direct test of the first effect, there is evidence that both AM fungi and rhizobia prime plant responses to pathogens (Pozo and Azcon-Aguilar, 2007; Zamioudis and Pieterse, 2012), which can lead to reductions in pathogen infection in hosts of both mutualists (Borowicz, 2001; Zamioudis and Pieterse, 2012). However, we do not know whether...
changes in pathogen resistance influence associations with AM fungi or rhizobia or whether there is an interaction between pathogen resistance and the priming effects produced by AM fungi and rhizobia. If it is possible to breed for reduced responses to pathogens together with increased response to AM fungi and rhizobia, then it might be possible to maintain, or even increase, crop production in a future with reduced fertilizer and agrochemical inputs (Fig. 3.1). However, breeding efforts will need to begin soon. Restrictions on many agrochemicals are already in place in the EU and elsewhere, peak phosphorus is expected to occur about 2030, and the availability of fossil fuels to provide the energy required for the Haber–Bosch process and the synthesis of agrochemicals is likely to peak shortly afterward (Raven, 2008). As a result, the general availability of fertilizers and agrochemicals is likely to decrease in the immediate future, and breeding programs will need to respond equally quickly to identify crop genotypes that yield well in a new agricultural environment.

ACKNOWLEDGMENTS

This work was supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government through Workpackage 3.3 (2011–2016). We thank James D. Bever for assistance in the development of Figure 3.2 and Euan James for his comments on the manuscript.

REFERENCES

Chapter 3 Benefits of Breeding Crops for Yield Response to Soil Organisms


