

The Impact of Beneficial Plant-Associated Microbes on Plant Phenotypic Plasticity

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Abstract Plants show phenotypic plasticity in response to changing or extreme abiotic environments; but over millions of years they also have co-evolved to respond to the presence of soil microbes. Studies on phenotypic plasticity in plants have focused mainly on the effects of the changing environments on plants' growth and survival. Evidence is now accumulating that the presence of microbes can alter plant phenotypic plasticity in a broad range of traits in response to a changing environment. In this review, we discuss the effects of microbes on plant phenotypic plasticity in response to changing environmental conditions, and how this may affect plant fitness. By using a range of specific plant-microbe interactions as examples, we demonstrate that one way that microbes can alleviate the effect of environmental stress on plants and thus increase plant fitness is to remove the stress, e.g., nutrient limitation, directly. Furthermore, microbes indirectly affect plant phenotypic plasticity and fitness through modulation of plant development and defense responses. In doing so, microbes affect fitness by both increasing or decreasing the degree of phenotypic plasticity, depending on the phenotype and the environmental stress studied, with no clear difference between the effect of prokaryotic and eukaryotic microbes in general. Additionally, plants have the ability to modulate microbial behaviors, suggesting that they manipulate bacteria, enhancing interactions that help them cope with stressful environments. Future challenges remain

in the identification of the many microbial signals that modulate phenotypic plasticity, the characterization of plant genes, e.g. receptors, that mediate the microbial effects on plasticity, and the elucidation of the molecular mechanisms that link phenotypic plasticity with fitness. The characterization of plant and microbial mutants defective in signal synthesis or perception, together with carefully designed glasshouse or field experiments that test various environmental stresses will be necessary to understand the link between molecular mechanisms controlling plastic phenotypes with the resulting effects on plant fitness.

Keywords Fitness · Mycorrhizal fungi · Nodulation · Phenotypic plasticity · Plant endophytes · Plant growth promoting rhizobacteria · Quorum sensing

Introduction

Plants have evolved with microbes over millions of years, and mycorrhizal fungi are likely to have co-evolved with plants for at least 400 MY, possibly enabling early land plant colonization (Pirozynski and Malloch 1975). Plants are almost universally colonized by endophytic and mycorrhizal fungi, by bacteria forming biofilms on root and leaf surfaces, bacteria living inside plant tissues as endophytes, nitrogen-fixing bacteria housed inside root or stem nodules, and many pathogenic organisms forming infection structures on leaves and in roots. Therefore, plants should always be considered to be colonized by microbes as the norm, not the exception (Partida-Martinez and Heil 2011). In some cases, plants have gained specific advantages from this intimacy with microbial partners, for example the delivery of fixed nitrogen and other nutrients and protection from pathogens. There is strong evidence that microorganisms affect plant fitness through direct or indirect effects on plant functional traits like nutrient provision, changes to photosynthesis, alteration of plant

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development and stress tolerance (Friesen et al. 2011; van der Heijden et al. 2008).

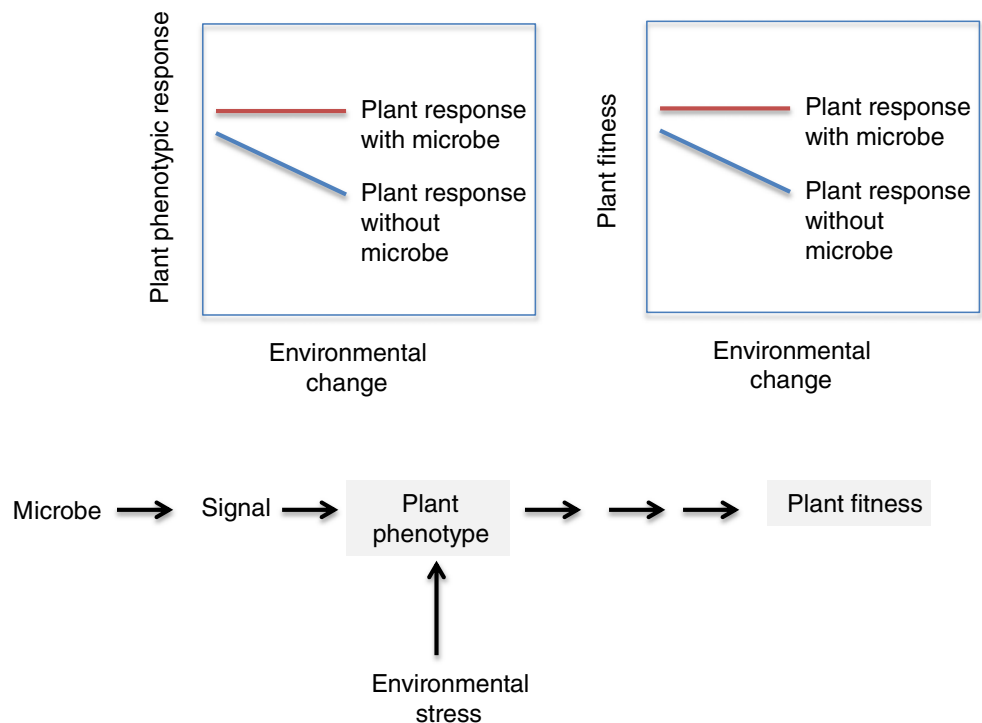
Prominent examples of plant-microbe interactions are the symbioses of plants with nitrogen fixing bacteria and with mycorrhizal fungi, which alter the ability of the plants to grow on low nutrient soils and offer pathogen protection. Nodulation in legumes with rhizobia enables plants to obtain nitrogen under low nitrogen availability, and it has been argued that this enabled legumes to have a ‘high nitrogen lifestyle’ (Mckey 1994). Mycorrhization in the majority of land plants has advantages in particular for phosphorus uptake (Smith and Smith 2011). Often the interaction with symbionts comes at some expense, e.g. in terms of carbon costs, towards the microbial partner. An interesting question arising from these interactions is whether microbes not only enhance growth, health, and fitness of the plant partner, but whether they also alter the degree of phenotypic plasticity in response to their environment, i.e., do microbes make plants more or less plastic in response to a changing environment, and are these changes in plasticity correlated with fitness such that the plasticity is adaptive (Fig. 1)?

In this review we examine plant-microbe interactions in which association with a microbial partner alters the pattern of plant responses to the environment. This is a complex area, as there are a number of pathways to plasticity. First, there is the direct plastic response of a plant to a microbe, which can lead to variation in the extent of symbiosis (nodulation level, for example depending on soil nutrient concentration). The primary impact of symbiosis is to alleviate

resource limitation to the plant and the plant can be expected to show a direct plastic response in traits to this change. However, recent work demonstrates that microbial symbionts can alter the pattern of the plant’s plastic response in more subtle ways than would be predicted if they are simply altering the resource environment.

Here, we first provide a general overview of our understanding of adaptive phenotypic plasticity with a focus on species interactions and plasticity. We then review several classes of plant-microbe interactions, focusing on mutualisms. In doing so we examine evidence for alteration in the expression of plasticity in the plant as a result of both direct and indirect effects of microbes on the plant and its environment. In particular, we are interested in whether the interaction between plants and microbes confers enhanced or altered plasticity in traits only indirectly related to the symbiotic relationship that then translate to increased plant fitness. Next, we examine how changes in plasticity are achieved by microbial signals, and explore the mechanisms underlying the interaction between microbial plasticity and plant plasticity. Finally, we discuss the complexity implicit in these systems, where one or more species of microbe and plant respond to and influence each other’s patterns of plastic response. We conclude with directions for integrative research bringing evolutionary and ecological perspectives on phenotypic plasticity together with investigations of the molecular and molecular genetic mechanisms that underlie plant microbe symbioses. While this is not an exhaustive review of the many examples of microbes that can affect

Fig. 1 Schematic depiction of the concept of plant phenotypic plasticity and how it is influenced by both the environment and the presence of microbes



plant phenotypic plasticity, we have chosen a range of examples that demonstrate the wide variety of phenotypic responses elicited by both prokaryotic and eukaryotic microbes.

Adaptive Plasticity and Plant Microbe Interactions

Phenotypic plasticity describes the environmentally induced variation in phenotype expressed by a genotype. Phenotypic plasticity is genetically controlled and heritable (Bradshaw 2006; Tuccic et al. 2005; Weijschede et al. 2006), can be altered in artificial selection experiments (Callahan and Pigliucci 2005; Garland and Kelly 2006; Kurashige and Callahan 2007), and is of potential importance to the ecology and evolution of species (Bradshaw 2006; Schlichting 2008; West-Eberhard 2005a, b). The diverse genetic architecture underlying plastic responses is rapidly coming to light and within species it is clear that there exists genetic variation in plasticity, e.g., through the presence or absence of receptors for environmental signals that can change under selection (Miner et al. 2005). Theory suggests that phenotypic plasticity will be particularly advantageous in heterogeneous environments (Sultan 1987; Valladares et al. 2000, 2002) and thus plasticity may provide plants with mechanisms to cope with changing environments, in addition to longer-term potential for adaptive evolution (Nicotra et al. 2010). Notably, although symbioses with microbes play an important role in mediating plant responses with the environment, the impact of plant microbe interactions on plasticity (in either player) has received markedly little attention to date.

Perhaps surprisingly, there have been relatively few clear demonstrations of the adaptive value of plant phenotypic plasticity in any traits. These are plastic responses that are associated with an increase in global fitness of the genotype (Dudley and Schmitt 1996; Schmitt et al. 2003; van Kleunen and Fischer 2005). To many this comes as a surprise because the adaptive value of plastic responses is often treated as a null hypothesis. Not all phenotypic responses to the environment, however, have fitness benefits. Some are neutral, others maladaptive, and yet others will be inevitable responses reliant on physical processes or resource limitation (van Kleunen and Fischer 2005). While the fitness benefits of microbial relationships are well demonstrated, there are no studies that we know of that directly test for an impact of a microbe on an adaptive plastic response in a plant trait.

To test an hypothesis of adaptive plasticity one must demonstrate that the expression of plasticity itself is correlated with some measure of fitness, and, therefore, potentially under selection, or one must demonstrate that the phenotype that maximizes fitness varies between environments (Caruso et al. 2006; Dudley and Schmitt 1996; van Kleunen and Fischer 2005; Weinig et al. 2004). Artificial selection on plasticity itself, or assessment of natural change in plasticity

in a population over time, add crucial evidence for adaptive plasticity, but few studies demonstrate these elements. Notably, adaptive plasticity may evolve as a result of direct selection on the plasticity or as a result of indirect selection on trait means, and the relative frequency of these pathways is unknown (Auld et al. 2010; van Kleunen and Fischer 2005; Via et al. 1995).

One challenge that arises in assessing the adaptive value of a plastic response is quantifying fitness by some measure (Davidson et al. 2011 and references therein). In a perfect world, fitness would be assessed by monitoring the rate of increase in a trait, or the number of successful offspring an individual with a trait has over several generations. However, a more practical approach is to identify good proxies of fitness; for example seed production or total plant biomass. These measures are particularly good proxies in annual plants. In the case of microbe/plant interactions, the impact of the symbiosis generally is assessed in terms of the biomass of the plant in the presence relative to absence of microbes, giving a ready proxy of fitness. These studies, however, often do not examine plastic changes in other traits that may confer the fitness homeostasis or fitness benefits. In contrast, assessments of plant responses to natural environments frequently assess plasticity in a broad range of morphological, anatomical, and physiological responses, but often without explicit comparison to a fitness proxy or for that matter consideration of the potential role of symbionts in mediating these plastic responses.

Among the best substantiated examples of adaptive phenotypic plasticity in plants are internode elongation in response to competition, and induced defenses to herbivores or pathogens. The former example is a simple one to begin with. Plants grown in the presence of competitors may show a shade avoidance response (stem elongation, decreased branch production) that can minimize shading from neighbors. This shade avoidance response increases fitness when light availability is limited by competitors. However, when plants are induced to produce the *inappropriate* phenotype (i.e., a short phenotype in a competitive environment, or an etiolated phenotype in a non-competitive environment), they suffer a reduction in fitness (Schmitt et al. 1999 and references therein). Thus, plasticity rather than the elongated phenotype, is an advantage. Note, however, that the value of the plastic response depends upon the cue (light quality) being a reliable indicator of competitive environment.

The case of induced plant defenses to herbivores or pathogens is more analogous to the plant microbe situation, but the cue generally is physical damage of plant tissue in response to which the plant produces a chemical or physical defense. The herbivore in some cases responds itself with altered digestive physiology that enables continued consumption of the plant (Agrawal 2001). The inducible nature of the defense is cost effective, and the adaptive value in

terms of reduction of tissue loss ('income' loss) and thus improved fitness homeostasis can be directly quantified. The implications of these interactions for the evolution of adaptive plasticity, genetic differentiation, and even speciation were well articulated more than a decade ago in the highly cited work of Agrawal (Agrawal 2001). Remarkably, however, neither that paper nor any of the hundreds of others that cite it directly examine interactions with microbial symbionts. Likewise, there is growing appreciation of the role that phenotypic plasticity plays in interactions among organisms, and how this may shape the evolution of community structure or composition (Berg and Ellers 2010; Fordyce 2006). But as of yet the role of microbial interactions *per se* has received little consideration.

Above, we posed the question of whether interactions with microbes will increase or decrease adaptive plasticity in plant traits. It is important to remember that plasticity is both trait and environment specific. In many cases, plasticity may evolve in some traits but not in others, such that plasticity in a given trait underlies homeostasis in another. In some contexts, plastic responses in a given trait are associated with a reduction in fitness. In these cases, selection would be expected to favor homeostasis, and often the canalization of those traits (Dejong 1995; Gomulkiewicz and Kirkpatrick 1992; van Buskirk and Steiner 2009; Via and Lande 1985). For example, plasticity in nodulation response in the presence of rhizobia may be accompanied by a reduction in plasticity of lateral root elongation, such that the nodulation plasticity has a fitness benefit, as does the relative canalization of lateral root elongation (Jin et al. 2012). In the examples below we will investigate whether there is a pattern in the degree that microbes change phenotypic plasticity in

plants, and we discuss examples of both prokaryotes and eukaryotes to examine whether there are any obvious differences in the effects of both types of organisms on plants.

Examples of Plant-Microbe Interactions that Alter Plant Phenotypic Plasticity and Fitness

In the following section, we highlight examples of plant-microbe interactions in which bacterial or fungal symbionts of plants have been shown to alter phenotypic plasticity of the plant host in response to changing environments. We examine, where known: (1) the microbial signals that trigger changes in plasticity; (2) which plant genes are involved in mediating the responses to the microbial signals; (3) which plant traits show plasticity; and (4) whether changes in plasticity have been linked to altered plant fitness. The studies are summarized in Table 1, and examples of changes in the degree of phenotypic plasticity elicited in the presence of microbes are depicted in Fig. 2.

Nitrogen-Fixing Symbioses

Nitrogen (N) is an important element for plant development, and is a major limiting factor for plant growth. All plants show phenotypic plasticity in response to soil N availability, and most of these involve changes in lateral root initiation and elongation, as well as root:shoot biomass allocation (Forde 2002). Root plasticity to nutrient availability is adaptive, and has been altered during plant domestication (Grossman and Rice 2012). Some plants have gained additional plasticity for dealing with N limitation by forming symbioses with nitrogen

Table 1 Examples of the influence of microbes on plant phenotypic plasticity in challenging environments

Environmental stress	Microbes that affect plant fitness	Microbial signal	Change in phenotypic plasticity achieved by the presence of the microbe	Increased fitness?
N limitation	Nitrogen fixing bacteria, (e.g. rhizobia)	Nod factors	Removal of N stress, resulting in a less plastic phenotype in response to the environment.	Yes usually
			Inhibition of morphological response to N, e.g. lateral root elongation	Unclear
P limitation	Mycorrhizal fungi	Myc factors	Removal of P stress, resulting in a less plastic phenotype in response to the environment. Changes in root morphology.	Yes usually
Fe limitation	PGPR (e.g. <i>Bacillus</i> spp.)	Organic volatiles	Alteration in root exudation (chemical plasticity) that enhances Fe availability for the plant, sometimes mediated by bacterial volatiles.	Yes
Abiotic stress (e.g. drought, salt, heat)	Fungal endophytes	Unknown	Changes in chemical plasticity to cope with stress, e.g. altered reactive oxygen species (ROS) production.	Yes
Biotic stress	PGPR (e.g. <i>Pseudomonas</i> spp; rhizobia spp. endophytes; mycorrhizal fungi)	Various, (e.g. quorum sensing signals, effectors, exopolysaccharides, many unknown)	Induction of Induced Systemic Resistance (ISR), leading to accelerated plant defence responses. Enhanced exudation of signals that attract beneficials to fight pathogen.	Yes usually

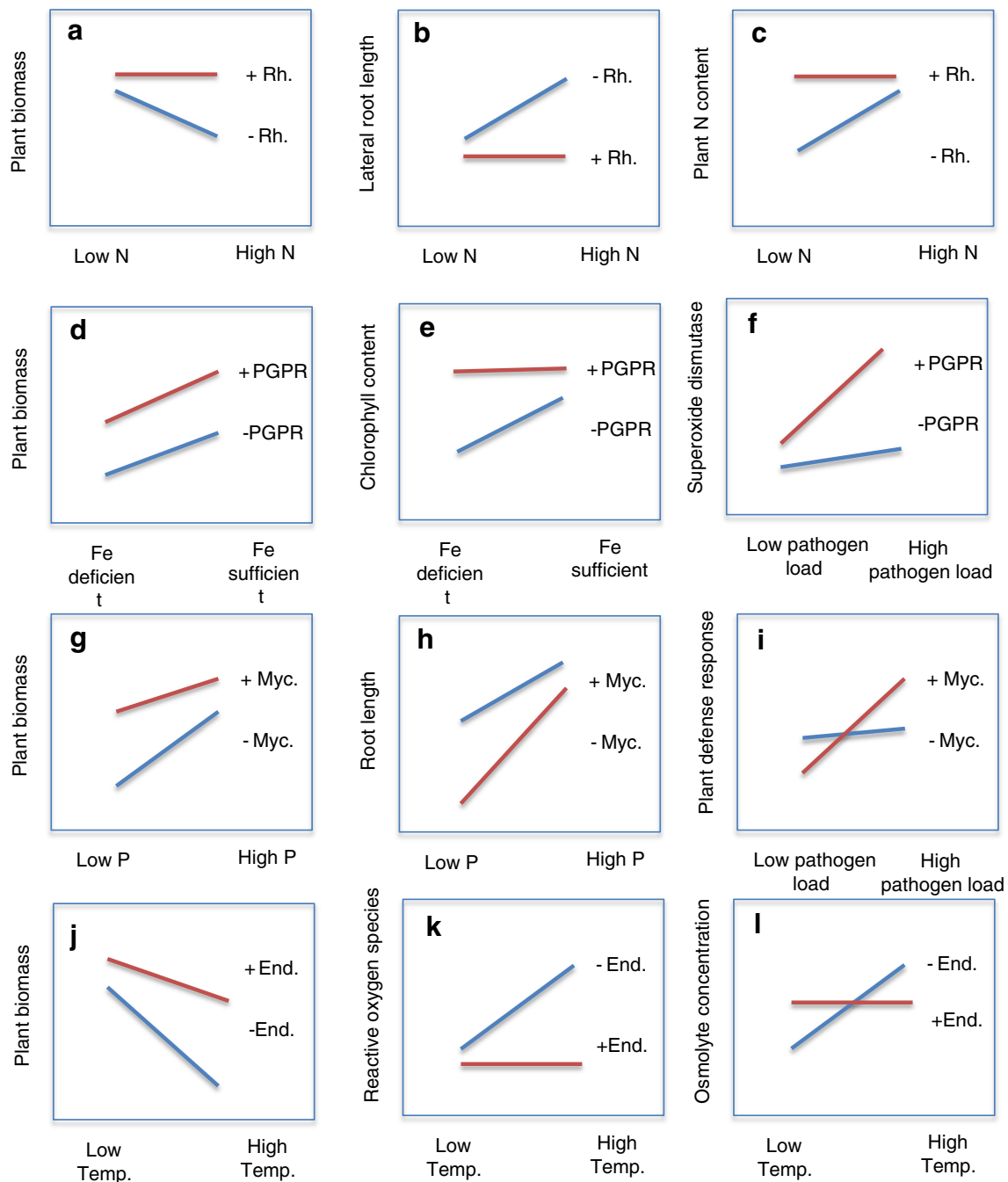


Fig. 2 Examples of the degree of change in the phenotypic plasticity through the influence of microbes. Each example shows the change in phenotypic plasticity to different environmental stresses in the presence, compared to the absence of a microbial partner. *Rh* rhizobia, *PGPR* plant growth-promoting rhizobacteria, *Myc* mycorrhizae, *End* fungal endophytes. Note that the responses shown are dependent on the

detailed conditions of each experiment and might vary. References for the responses are as follows: **a** Wang et al. (2011); **b** Jin et al. (2012); **c** Wang et al. (2011); **d** Orozco-Mosqueda et al. (2013); **e** Orozco-Mosqueda et al. (2013); **f** Pandey et al. (2012); **g** Wang et al. (2011); **h** Wang et al. (2011); **i** Sikes et al. (2009); **j** Rodriguez et al. (2008); **k** Rodriguez et al. (2008); **l** Redman et al. (2011)

fixing bacteria, which leads to the formation of root nodules that house the symbionts (Oldroyd 2013). The provision of fixed N by the microbes is balanced with the supply of fixed carbon from the plant host (White et al. 2007). Of particular importance are rhizobia, which form a symbiosis with legumes,

and the actinomycete *Frankia* that forms symbioses with a number of plant genera called ‘actinorhizal plants’ (Pawlowski and Bisseling 1996).

The evolution of legume nodulation approximately 60 MYA was likely a response to a changing climate, as it occurred at a

time of increasing atmospheric CO₂ concentrations, thus enabling legumes to benefit from higher CO₂ concentrations by increasing their N nutrition (Sprent 2007). While the symbiosis generally is thought to be mutualistic, it can be viewed as a form of parasitism (Djordjevic et al. 1987) because the symbiont requires large amounts of carbon from the host, and varying degrees of parasitism can be observed (e.g., Barrett et al. 2012; Thrall et al. 2011). Nevertheless, in most cases, the symbiosis increases plant fitness under N limiting conditions.

There are at least three mechanisms by which rhizobia are able to increase plant fitness under N stress: (1) the fixation of atmospheric nitrogen can provide N nutrition under low N conditions; (2) the rhizobia can have effects on root architecture that might indirectly lead to better growth and fitness in some environments; and (3) the rhizobia can confer a degree of resistance to pathogens.

The ability to form nodules at times of low soil N availability is a form of plasticity gained by legumes and actinorhizal plants that has allowed fitness increases. Nodulation is dependent on the synthesis of specific Nod factor signals by rhizobia (Spaink 1996), which are perceived by Nod factor receptors by the host (Oldroyd 2013). The obvious plant trait altered by Nod factor signaling is root architecture, i.e., formation of a new root organ, the nodule, accompanied by changes in lateral root formation (Olah et al. 2005). The changes in nodule formation are strongly dependent on the N availability, as nodule development is inhibited in the presence of N (Streeter 1988). Infection of legumes with rhizobia usually leads to higher, and more stable, plant biomass of inoculated plants under low and high N availability, whereas in uninoculated plants the biomass is more responsive to N availability (e.g., Richardson et al. 1957; Wang et al. 2011). The same trend is seen for N content of the plant host, suggesting that biomass changes in response to N are buffered through directly alleviating the N stress by nitrogen fixation. The fitness outcome for the host depends on the infecting strain of rhizobia, which vary in their degree of nitrogen fixation (Burdon et al. 1999). The ability of plants to actively sanction nodules that are ineffective in nitrogen fixation demonstrates the extent of host control of the symbiosis (Denison 2000; Kiers and Denison 2008).

Apart from direct effects of N availability to the plant host, rhizobia have indirect effects on host root architecture. A study by Jin et al. (2012) tested a number of plant phenotypes of *Medicago truncatula* in response to nitrate availability in the presence and absence of rhizobia. In general, phenotypic plasticity to N, e.g., root length, lateral root density, and root-shoot ratio were significantly influenced by N availability. The presence of rhizobia significantly hampered the ability of the host to increase lateral root length and to reduce lateral root density in response to increasing nitrate. Plant genotype also had a significant effect on the ability of rhizobia to alter plant phenotypic plasticity. The supernodulation mutant

sunni had lost the ability to alter root length and lateral root density in response to nitrate treatments, and this was associated with altered responses to rhizobia (Jin et al. 2012). *SUNNI* is a gene that regulates nodule numbers through a systemic signaling mechanism called autoregulation (Reid et al. 2011). Thus, *SUNNI* is likely to modulate plant phenotypic plasticity in response to N limitation in the presence of rhizobia. Reduced phenotypic plasticity in response to N in *sunni* was correlated with reduced plant fitness compared to the wild-type, as assessed by biomass production of shoot and root. Soybean autoregulation mutants similarly showed decreased fitness in long-term field trials, even though their nodulation was higher than that of wild-type plants (Song et al. 1995), presumably because of the high cost of nodule formation for the host. While purified Nod factors were shown to have effects on root branching (Olah et al. 2005), the above-mentioned experiments were performed only with wild-type rhizobia. It would be interesting to test whether nodulation deficient rhizobial mutants are ineffective in altering root plasticity in varying N environments to determine the contribution of rhizobial signals compared to plant genes in the phenotypic outcomes.

Overall, to test whether Nod factor signaling causes changes in phenotypic plasticity and whether that results in enhanced adaptive plasticity, one would need to grow legumes with varying ability to respond with phenotypic changes to rhizobia (i.e., supernodulating or non-nodulating mutants) under a range of N concentrations and in the presence and absence of rhizobial mutants that vary in their ability to produce Nod factors. The changes in phenotypic plasticity in response to the changes in environment, e.g., lateral root architecture, then would need to be compared to the ability of the respective treatment to cause fitness advantages, i.e., higher biomass or seed yield, preferably over several generations.

Apart from direct effects of rhizobia on plant growth via provision of N and alteration of root architecture in N-limiting environments, rhizobia also indirectly benefit plants by providing protection from pathogens (discussed below in the section on plant growth-promoting rhizobacteria) and herbivores. The latter example is interesting because it links the provision of nitrogen with herbivore protection: Some plants produce nitrogen-containing cyanogenic glycosides that repel leaf-chewing insects. A study of the tripartite interaction between lima bean, rhizobia, and the Mexican bean beetle found that rhizobia-inoculated plants produced substantially more cyanogenic glycosides than non-nodulated plants, and this was associated with higher shoot biomass and a significant reduction in the leaf area consumed by the beetle (Thamer et al. 2011). To demonstrate conclusively that this chemical plasticity is adaptive, it would be necessary to test if a plant mutant unable to form cyanogenic glycosides or unable to respond to rhizobia with its production, would also be unable to confer a fitness advantage.

Plant Growth-Promoting Rhizobacteria (PGPR)

Another group of bacteria, loosely defined as plant-growth promoting rhizobacteria (PGPR), can significantly enhance plant growth through increasing nutrient availability, stimulating root branching for better soil exploration, or protecting plants from pathogens, either directly through producing antibiotics and hormones or through modulation of host immunity (Berendsen et al. 2012; Lugtenberg and Kamilova 2009). Some of this cross-protection involves highly evolved changes in chemical plasticity by both plant and bacterial partners. For example, bacterial and plant organic volatiles can each play a role in enabling plants to colonize nutrient poor soils, as demonstrated by experiments involving the co-cultivation of plants and bacteria in partitioned plates to exclude physical contact, i.e., communication by both partners occurs only by volatile compounds. Volatiles have been shown to be particularly important for iron acquisition with effects on photosynthesis. Volatiles produced by the PGPR *Bacillus subtilis* in the presence of *Arabidopsis thaliana* enhance proton release by the plant in Fe-deficient growth media, and this response is mediated by the Fe-deficiency Induced Transcription Factor FIT1 (Zhang et al. 2009). The increased Fe content of plants treated with *B. subtilis* volatiles is correlated with higher chlorophyll content, higher photosynthetic efficiency, and increased plant size (Zhang et al. 2009), suggesting an effect on plant fitness. Similar effects on iron nutrition have been shown in *M. truncatula* in the presence of its symbiont *Sinorhizobium meliloti* (Orozco-Mosqueda et al. 2013). Volatiles of *Bacillus* strains and other PGPRs also have been shown to alter root architecture in *A. thaliana* by changing primary and lateral root length and density (Gutiérrez-Luna et al. 2010). This impact has not been assessed in response to varying environments, thus the interaction between soil resource availability and the symbiosis is unknown. The ability to alter root architecture in response to the environment, e.g., nutrient availability, is a plasticity phenotype that can be associated with higher fitness outcomes (Fitter et al. 2002).

PGPR microbes also can indirectly benefit plant fitness through control of harmful soil organisms, a process that is responsible for the build-up of disease suppressiveness in soils. A prominent example is fluorescent *Pseudomonas* species that suppress take-all disease caused by the fungus *Gaeumannomyces graminis* var *tritici* by synthesizing the antifungal compound 2,4-diacetylphloroglucinol (Raaijmakers and Weller 1998). PGPR also have demonstrated effects on plant immunity, i.e., their presence influences the plant's plasticity towards biotic stress, enhancing plant survival. PGPR modulate plant immunity by stimulating 'induced systemic resistance' (ISR) towards pathogens. This mechanism involves priming for accelerated defense gene expression in case of a pathogen attack following exposure to the PGPR. ISR induction has been demonstrated in

response to PGPR bacteria, as well as fungal endophytes and mycorrhizal fungi (reviewed by Berendsen et al. 2012; Zamioudis and Pieterse 2012; see also Song et al. 2013).

An example of how a PGPR alleviates biotic and abiotic stress in plants is the interaction of *P. aeruginosa* with plants. Several studies with *P. aeruginosa* have shown it to boost ISR in diverse plant species (Audenaert et al. 2002; De Meyer and Hofte 1997; De Vleeschauwer et al. 2006) under biotic and abiotic stress through secondary metabolites that act as inducers of plant resistance (Verhagen et al. 2010). For instance, *P. aeruginosa* PW09 strain isolated from wheat stem, altered cucumber (*Cucumis sativus*) plant fitness under salt stress, reducing seedling mortality by 60 %, and significantly increasing the accumulation of biomass and vigor in comparison with untreated plants (Pandey et al. 2012). Khalimi and Suprpta (2011) demonstrated that *P. aeruginosa* increased soybean resistance against soybean stunt virus and significantly increased the maximum plant height, fresh and dry shoot and root biomass under greenhouse conditions. The authors also found a significant increase in seed biomass (a potential indicator of plant fitness). Several studies have suggested that *P. aeruginosa* effects on plant performance under biotic and abiotic stress are controlled by the production of virulence factors, either antibiotics or iron-scavenging siderophores, which are controlled by quorum sensing signaling (Jiricny et al. 2010; Khalimi and Suprpta 2011; Saharan and Nehra 2011). This chemical signaling can cause plasticity in the plant in terms of secondary metabolite synthesis, such as proline, phenolics, pyochelin, phytoalexins, and/or changes in reactive oxygen species (ROS) production (Audenaert et al. 2002; Pandey et al. 2012; Verhagen et al. 2010). As for nodulation, it will be important in the future to examine the phenotypic plasticity and fitness responses of wild-type compared to mutant plants unable to respond plastically to microbes under environmental stress to more clearly test whether changes in phenotypic plasticity are linked to fitness advantages.

Mycorrhizal Symbioses

Mycorrhizal fungi usually form mutualistic symbiotic relationships with plants that enable plants to scavenge inorganic phosphorus (Pi), N, zinc, and other nutrients from the soil, and also improve water uptake (Harrison 2005). Mycorrhizal relationships have enabled plants to grow on low-phosphorus (P) soils and resist a number of environmental stresses (Barea et al. 2002), although the interaction also can be negative depending on environmental conditions and costs associated with the symbiosis (Johnson et al. 1997), e.g., mycorrhizal infection can decrease direct Pi uptake from the soil by the plant (Smith and Smith 2011). Mycorrhizal fungi produce signals (Myc factors) that are similar to the lipochitin oligosaccharide Nod factors that are synthesized by rhizobia (Maillet et al. 2011), but because of the complex genetic

nature of mycorrhizal fungi, no Myc factor deficient mutants are available yet to study the direct effect of Myc factors synthesized by the fungal symbiont on plant phenotypic plasticity. In contrast, plant mutants defective in mycorrhizal signaling are available, and several of these early signaling genes are the same as those required for nodulation in legumes (Oldroyd et al. 2009).

Infection of plants with mycorrhizal fungi can cause significant changes in plant growth and morphology characteristics, including shoot and root weight, flower number, time to flowering, and seed N and P content (e.g., Berta et al. 1995; Lu and Koide 1994). An example of the effect of mycorrhizal fungi on plant fitness is provided by a study in which infection of *Abutilon theophrasti* with *Glomus etunicatum* led to higher plant productivity under limiting P concentrations, and improved fitness homeostasis in response to varying P compared to non-infected plants (Lu and Koide 1994). These studies were inconclusive as to whether this is simply a direct effect of better nutrition or whether phenotypic plasticity of morphological traits induced by the fungus indirectly resulted in improved plant growth.

Mycorrhizal fungi specifically induce the formation of lateral roots in their hosts, thus increasing growing roots available for colonization (Harrison 2005; Olah et al. 2005; Price et al. 1989). A study in maize showed that enhanced root growth in mycorrhizal compared to non-mycorrhizal wild-type plants was associated with increased shoot growth under P limiting conditions (Paszkowski and Boller 2002). Interestingly, a maize mutant defective in lateral root formation could be rescued by infection with mycorrhizal fungi under low P conditions, forming short, branched root systems and vigorous shoots (Paszkowski and Boller 2002). Shoot weight of the mutant plants grown under low P was higher than that of uninfected mutant plants grown under high P, with much lower shoot weight in uninfected mutants grown under low P, suggesting that increased shoot biomass is caused by a combination of mycorrhizal effects on root architecture and P uptake. Another study with legume root architecture mutants has shown no clear link between plant P content and shoot biomass, but has demonstrated correlations between altered root morphology and shoot dry weight. However, a clear link between mycorrhizal effects on root morphology under different P conditions was not tested in that study (Schultz et al. 2010). A recent study in tobacco suggested that the effect of mycorrhizal fungi on root morphology under varying P levels is linked to higher shoot weight and that this effect is mediated by cytokinin signaling (Cosme and Wurst 2013).

Some studies have examined whether the effects of mycorrhizal fungi on root plasticity are dependent on Myc factor signaling. One that compared the ability of the mycorrhizal fungus *Glomus intraradices* to induce lateral roots in

M. truncatula mutants defective in Myc factor signaling showed that all non-mycorrhizal mutants used were able to respond to the fungus with increased lateral root formation, suggesting signals other than Myc factors are responsible for lateral root alterations. However, this effect was not tested under varying P conditions, and no link to fitness was made (Gutjahr et al. 2009). With the identification of Myc factors, the role of synthetic Myc factors on root architecture was tested and all known early Myc and Nod factor signaling mutants of *M. truncatula* were found defective in lateral root plasticity in response to Myc factors (Maillet et al. 2011). Myc factors also were shown to enhance root colonization of the fungus, but this might not necessarily lead to increased plant fitness. The study by Maillet and colleagues again did not test whether lateral root formation or fungal root colonization in response to Myc factors varied in different (P) environments and whether the changes in lateral root formation caused increased fitness. These experiments will need to be carried out in the future to test whether the changes in phenotypic plasticity caused by mycorrhizal fungi, and Myc factors in particular, are adaptive to a changing environment. The use of a large range of mycorrhizal and root architecture mutants will help in identifying the genes and pathways in the plant responsible for mediating the plasticity effects on fitness.

Mycorrhization also affects interactions of plants with rhizobia in changing N environments. For example, mycorrhization can alleviate the inhibition of nitrogen fixation by external Vazquez et al. (2002) demonstrated that co-inoculation of alfalfa with rhizobia and mycorrhizal fungi led to both greater N and P use efficiency and plant growth in response to external ammonium nitrate compared to non-mycorrhizal roots (Vazquez et al. 2002). Similarly, in the common bean, inoculation of roots with both mycorrhizal fungi and rhizobia maintained nodule function (nodule mass and nitrogen fixation) at moderate (1 mM) ammonium concentrations that inhibited nodule function in non-mycorrhizal roots (Mortimer et al. 2012). This could be due to a reduced N feedback inhibition of nodulation by asparagine formed in mycorrhizal infected roots, which show lower accumulation of asparagine than non-AM roots under elevated external ammonium supply (Mortimer et al. 2012; Sulieman et al. 2010). The co-inoculation of plants with rhizobia and mycorrhizal fungi resulted in higher root respiration and photosynthesis rates compared to rhizobia infected, non-mycorrhizal plants, but whether mycorrhization resulted in higher fitness was not determined in this study (Mortimer et al. 2012).

Mycorrhizal fungi also mediate increased resistance, i.e., increased plasticity in biochemical defense responses, of plants towards pathogens. Studying plant protection against the fungal pathogen *Fusarium oxysporum*, Sikes and colleagues showed that different species of mycorrhizal fungi differed significantly in their ability to reduce *F. oxysporum*

colonization, and this protective effect was strongly correlated with mycorrhizal infection of the roots, as well as with resulting plant biomass (Sikes et al. 2009). Similarly, mycorrhizal isolate identity was found to be a strong determinant of plant protection from the root pathogen *Rhizoctonia solani*, alleviating shoot and root weight losses from the pathogen (Volpin et al. 1995). In that study, the alleviation of pathogen symptoms was associated not with changes in root architecture induced by the mycorrhizal partner, but with reallocation of resources between shoot and root, which may allow the plant to stimulate mycorrhizal proliferation in the root, presumably with beneficial effects on nutrition. While the exact mechanism of plant protection from the pathogen through the presence of mycorrhizal fungi is not known, it is likely that it results from a combination of better nutrition and effects of the mycorrhiza on inducing plant defense responses (Campos-Soriano et al. 2012; Vos et al. 2012).

Fungal Plant Endophytes

Fungal endophytes have been identified as driving factors behind abiotic stress tolerance in many plants. The establishment of fungal endosymbiosis with plants was termed ‘habitat-adapted symbiosis’ because the symbioses often are formed under conditions of high abiotic stress, e.g., heat, salt, or disease (Redman et al. 2002, 2011; Rodriguez et al. 2008). Fungal endophytes including *Colletotrichum*, *Curvularia*, and *Fusarium* species, that were collected from hot, highly salty, or high disease load environments were found to confer heat, salt, or disease tolerance to plants in those environments, as well as to crop plants, e.g., rice and tomato inoculated with those adapted strains (Rodriguez et al. 2008). In this case, the enhanced fitness is inferred from higher plant survival, increased plant health and biomass formation. It would be interesting to test whether inoculation of plants with these habitat-adapted symbiotic fungi specifically affects plasticity in traits that underlie the biomass response: e.g., root:shoot allocation or differences in root or shoot branching in response to varying levels of stress. Part of the chemical plasticity response likely is to involve the regulation of reactive oxygen species (ROS), as symbiotic plants produced less ROS than non-symbiotic plants (Rodriguez et al. 2008). In the future, it will be interesting to identify the endophyte signals responsible for altering the physiological responses of plants to abiotic stresses.

As was seen for interacting rhizobia and mycorrhizae above, in some cases, it is likely that interactions with other organisms influence the relationship between endophytic fungi and plants. For example, the ability of the plant-associated fungus *Curvularia protuberata* to confer heat tolerance to its plant partner, the tropical grass *Dichantherium lanuginosum* that grows on geothermal soils, depends on the presence of a virus residing inside the fungus (Marquez et al. 2007).

Similar to other mutualistic organisms, fungal endophytes also can alleviate pathogen and herbivore stress on plant hosts (Gundel et al. 2012; Rodriguez et al. 2009), but the mechanisms and ecological consequences are not well understood (see also Saikkonen et al. 2013).

Plants Actively Control Bacterial Behaviours that can Influence Plant Fitness

There is compelling evidence that plants benefit from microorganisms in coping with environmental stress, by influencing them through exudation of chemical signals into the soil. It is estimated that between 5 % and 30 % of fixed carbon is exuded into the soil (Marschner 1995). Changes in root exudation can have major effects on the microbial community structure in the soil (Badri et al. 2009), and this potentially could alter the balance of beneficial to harmful microbial species surrounding the root. An example of how a change in exudation helps the plant cope with biotic challenges was demonstrated in *A. thaliana*. Foliar inoculation of *A. thaliana* with the leaf pathogen *P. syringae* pv tomato stimulated the secretion of malic acid by the roots, which in turn attracted the PGPR *B. subtilis* that caused ISR towards the pathogen (Rudrappa et al. 2008). It would be interesting to investigate whether there is plant genetic variation in the ability to change malic acid production in response to bacterial signals, in order to determine whether plants with enhanced ability to modulate root exudation have greater survival.

Another example is the regulation of flavonoid exudation by legumes and the recruitment of symbiotic rhizobia. Flavonoid exudation is increased in the absence of available N in the growth medium, i.e., at a time when the plant requires the nitrogen-fixing symbiosis (Coronado et al. 1995). The exuded flavonoids not only attract rhizobia to the root, but also are required for the transcriptional activation of *Nod* genes in rhizobia (reviewed by Cooper 2004). There is further feedback between the plant host and rhizobia, as the latter stimulate further flavonoid synthesis that enhances the initial *Nod* gene induction (e.g., Schmidt et al. 1994).

Plants also interfere with bacterial quorum sensing, and this can alter bacterial behaviors leading to changes in symbiosis or pathogenesis, as quorum sensing signaling is important in host colonization, virulence, and nitrogen fixation (Fig. 3; Gonzalez and Marketon 2003; Miller and Bassler 2001). A range of plants has been found to exude signals that either stimulate or inhibit quorum sensing signaling in bacteria (Gao et al. 2003; Teplitski et al. 2000). The production of quorum sensing mimics was enhanced after perception of purified quorum sensing signals by the plant, and differed in response to different structures of quorum sensing signals (Mathesius et al. 2003). However, so far no studies have tested whether plants with varying capacities to exude quorum sensing mimics differ

in their ability to withstand environmental stress due to lack of microbial coordination.

Future research will require detailed studies on whether the perception and response by plants to microbial signals confers fitness advantages under a range of environments and whether this is mediated by changes in plant phenotypic plasticity in other traits. For example, if plants change root exudation in response to Nod factors or quorum sensing signals, does this confer fitness under varying soil nutrient deficiencies or in the presence of harmful microbes? It also will be important to find out which plant genes and proteins, e.g., receptors, enable plants to respond to the large number of signals from microbes, and whether and how these genes and gene products are linked to changes in morphological or chemical phenotypic plasticity. Screening of plants for their ability to respond to bacterial signals or bacterial volatiles will be critical for our understanding of how perception of bacterial signals is linked to changes in plasticity and fitness.

The fact that plants “manipulate” bacterial populations thus improving their own performance suggests that they are not merely “coerced” into changing their phenotype in response to microbial signals, but that they “control” their phenotype. However, to test this hypothesis, one would need to demonstrate that a plant mutant defective in exudation of

specific signals also is defective in benefiting from the presence of the interacting microbes.

Conclusions and Future Directions

In conclusion, we have presented some examples of how plant fitness, or fitness proxies, in challenging environments are altered by association with microbial partners, and in some cases, how that has been achieved through changes in plant phenotypic plasticity to the environment. While, in general, symbiotic microbes enhance plant fitness of their host in challenging environments, the variety of the changes in phenotypic plasticity elicited by microbes depicted in Fig. 2 demonstrate that there is no common pattern in how the degree of phenotypic plasticity is changed by microbes. Rather, it depends on the phenotype examined whether microbes increase, decrease or maintain the degree of phenotypic plasticity (i.e. the slopes of phenotypic change in response to a gradient in the environment) in a certain plant species under environmental stress. There also is no clear difference between the types of responses elicited by prokaryotic (rhizobia and PGPR) and eukaryotic microbes (mycorrhizal and endophytic fungi).

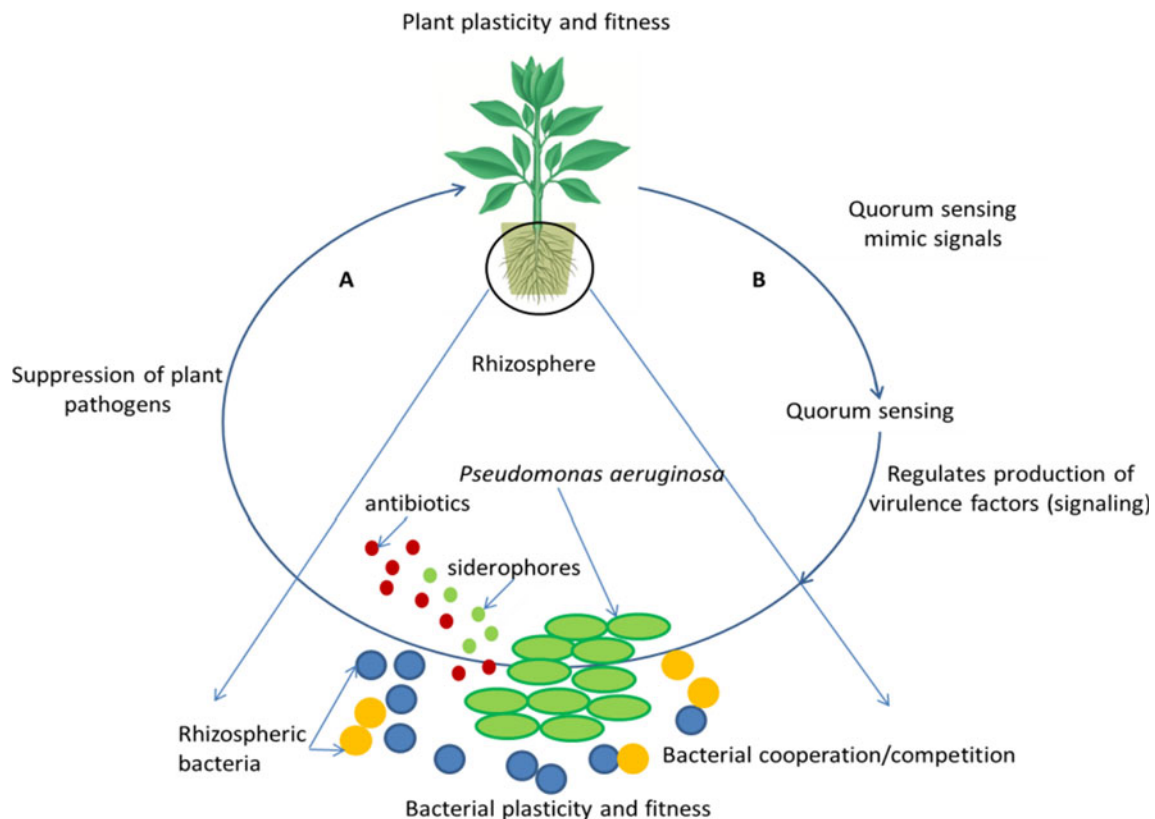


Fig. 3 Depiction of the communication between plant and microbes in which plant exudates alter the behavior of microbes in the rhizosphere which in turn can affect plant performance through production of nutrients, hormones, virulence factors, siderophores, and other factors by the microbe

The mechanisms that mediate microbial effects on plant plasticity and fitness include *direct* mechanisms, i.e., attenuation of the environmental stress by the microbes by providing nutrients under nutrient limiting environments. They also include *indirect* mechanisms, for example, the altered morphological responses to the environment, the alteration of chemical exudation by the plant in response to microbial signals, and changes in plant physiology (e.g., production of reactive oxygen species) that cope with biotic or abiotic stress (Table 1).

The findings that plants enhance interaction with microbes that alter their response to the environment, for example by recruiting specific microbes through exudation of signal molecules into the rhizosphere, suggest possible avenues to improve the influence of microbes on plant fitness in changing environments. It would be interesting to test first whether there is genetic variation for exudation of signals to soil microbes, and if so, whether in multigenerational experiments plants change exudation patterns of certain signal molecules that lead to enhanced colonization and altered plant responses to changing environments.

Where to from now? So far, few studies have investigated in any systematic manner whether it is the changes in plasticity (morphological or chemical) that alter plant fitness in response to the interaction with microbes, primarily because plant mutants unable to respond to microbes with altered phenotypic plasticity have not been available or have not been investigated. While many studies have focused on plant plasticity in a changing environment and how this alters plant fitness, these studies generally have not taken into account the presence of microbes in the environment. On the other hand, studies examining how microbes affect plant responses to the environment mostly do not specifically test for impacts on plant plasticity in other traits or on detailed assessments of fitness. We recommend that future research should combine studies on plant-environment-microbe interactions such that morphological, chemical, and/or physiological plasticity changes in response to microbes can be linked to fitness in a changing environment. These three level studies are necessary to identify the molecular/genetic architecture underlying the plastic response. Until this type of study is conducted, we cannot gauge the extent to which the microbe directly affects plant plasticity in traits not directly related to the symbiosis versus the microbe altering the resource environment and thus eliciting an indirect effect. Evidence presented above suggests the former is widespread. Thus, research into the evolution and genetic control of these interactions promises to be exciting.

To advance our understanding of the mechanisms by which microbes alter phenotypic plasticity, we will need to discover: (1) what the bacterial signals are that affect plant phenotypic plasticity; (2) which plant genes allow plastic responses to microbial signals (e.g., receptors); (3) how the

perception of the microbial signal alters plant traits under changing environmental conditions; and (4) how these phenotypic changes translate into altered fitness. The *Rhizobium*-legume symbiosis would be a good model for trying to get a comprehensive picture of these different aspects because (a) mutants of rhizobia that lack various signals, e.g., Nod factors, exopolysaccharides, quorum sensing signals, are available, (b) plant mutants lacking receptors to microbial signals, e.g., Nod factor deficient mutants, autoregulation mutants, also are available, (c) the symbionts can be grown under controlled conditions and a number of traits, e.g., nutrient content, root architecture, changes in defense responses and resulting plant fitness can easily be monitored.

While the use of such model systems will be useful in studying single plant-microbe interactions, the complexity of this area has so far been vastly underestimated. Studies in which plant-associated microbes have been identified by high throughput sequencing have estimated that a plant could be colonized by thousands of bacterial species inside and on the surface of its tissues (Bulgarelli et al. 2012; Lundberg et al. 2012; Peiffer et al. 2013). Most studies that have examined the effect of microbial partners on plant phenotypic plasticity have involved only one or two microbes under controlled conditions. One challenge for the future will be to carry out studies with complex mixtures of microbes associated with plants, for example by assessing the phenotypic plasticity of plants in response to whole microbial communities associated with certain stressful environments (Pendergast et al. 2013). The important applications in this area are to use microbial inoculants, together with plant genotypes that respond optimally, to help plants perform better in a more variable environment.

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