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REVIEW ARTICLE

Novel approaches in plant breeding for rhizosphere-related traits

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Abstract Selection of modern varieties has typically been performed in standardized, high fertility systems with a primary focus on yield. This could have contributed to the loss of plant genes associated with efficient nutrient acquisition strategies and adaptation to soil-related biotic and abiotic stresses if such adaptive strategies incurred a cost to the plant that compromised yield. Furthermore, beneficial interactions between plants and associated soil organisms may have been made obsolete by the provision of nutrients in high quantity and in readily plant available forms. A review of evidence from studies comparing older traditional varieties to modern high yielding varieties indeed showed that this has been the case. Given the necessity to use scarce and increasingly costly fertilizer inputs more efficiently while also raising productivity on poorer soils, it will be crucial to reintroduce desirable rhizosphere-related traits into elite cultivars. Traits that offer possibilities for improving nutrient acquisition capacity, plant–microbe interactions and tolerance to abiotic and biotic soil stresses in modern varieties were reviewed. Despite the considerable effort devoted to the identification of suitable donors and of genetic factors associated with these beneficial traits, progress in developing improved varieties has been slow and has so far largely been confined to modifications of traditional breeding procedures. Modern molecular tools have only very recently started to play a rather small role. The few successful cases reviewed in this paper have shown that novel breeding approaches using molecular tools do work in principle. When successful, they involved close collaboration between breeders and scientists conducting basic research, and confirmation of phenotypes in field tests as a 'reality check'. We concluded that for novel molecular approaches to make a significant contribution to breeding for rhizosphere related traits it will be essential to narrow the gap between basic sciences and applied breeding through more interdisciplinary research that addresses rather than avoids the complexity of plant–soil interactions.

Keywords Beneficial rhizobacteria · Mycorrhizal fungi · Nutrient acquisition · Nutrient deficiency · Nutrient toxicity · Soilborne disease tolerance

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Introduction: plant breeding and the rhizosphere—a historical perspective

Agriculture in the twentieth century was characterized by impressive productivity gains. During the past 4 decades global food production has more than doubled and outpaced population growth (Evenson and Gollin 2003). Most of that increase has been due to a sharp rise in crop yields as a result of a bundle of "Green Revolution" technologies, namely improved varieties, increased fertilizer and pesticide use, and improvements in water supply through irrigation. The contribution of improved varieties to yield increases varied between crops and regions with estimates typically ranging from 30–50% (Evenson and Gollin 2003; Khush 1999; Tilman et al. 2002).

During the next four decades global population is projected to increase by 30–50%, which will require, at minimum, an equally large increase in food production to avert widespread malnutrition (Tilman et al. 2002). This increase in production will most likely be dependent upon a diminishing area of highly productive land, not only as a result of agricultural land being diverted to other uses but also due to the recent land-use change from food production to production of renewable energy resources. The need to increase yields further therefore seems to be a necessity. However, in many of the most productive environments crops have reached a yield ceiling (Duvick and Cassman 1999) and unless new means are found to overcome this barrier much of the additional food production will have to come from less favorable environments where nutrient deficiencies and toxicities are a significant obstacle.

Thus, the main present day challenges in agriculture can be summarized as (1) continued expansion of production to feed a growing population, (2) to do so in a more sustainable manner that reduces environmental impact, (3) to improve living standards for rural poor in developing countries, and (4) provide staple food crops with higher micronutrient content. Meeting these challenges will require new approaches and in that context the often overlooked role of rhizosphere traits in breeding programs will be the topic of this review.

The global shift towards sustainable agricultural production systems that do not compromise environmental or human health will necessitate reduced reliance on fertilizer and pesticide inputs in regions of high crop productivity. Maintaining high yield levels under sustainable systems will require gains to be made in nutrient efficiency traits. Attempts to achieve this goal have primarily focused on maintaining high yields with reduced nitrogen (N) inputs, either through selection of genotypes with higher N use efficiency (Bänziger et al. 1997; Presterl et al. 2002) or through enhancing microbial conversion of atmospheric N_2 to a plant usable N form. However, the realization that phosphorus (P) fertilizers are a finite resource that will be depleted towards the end of this century (Runge-Metzger 1995) is going to make improvements in P efficiency a necessity. Attention should therefore focus on improving the abilities of crop plants to access soil-bound P, and other nutrients, that have accumulated as a result of continued fertilization (Vance et al. 2003). A focus on sustainable agriculture will also dictate reduced pesticide application. One opportunity that has received minimal attention in this realm is the management and enhancement of native rhizosphere associated microbial communities that are antagonistic toward pathogens. Breeding efforts are in their infancy but this is an exciting new field as recent studies have demonstrated the genotype specific nature of interactions with these saprophytic microorganisms.

If plant breeding is to play a crucial role in providing varieties that are highly productive with reduced fertilizer and pesticide inputs, it will be important to examine past effects of breeding on rhizosphere function prior to developing novel approaches for plant breeding. In this paper we will first review some of the historic developments with regard to the effect of plant breeding on rhizosphere-related traits and then proceed to identify potentially useful traits for assimilation into breeding programs. Additional related processes such as root growth, architecture and development affect the development of the rhizosphere over space and time (Hinsinger et al. 2005). As such, the following discussion will extend beyond the traditional definition of rhizosphere traits to include specific elements which have definitive impacts on the structure and function of the rhizosphere. Our discussion will conclude with an outline of possible breeding strategies to incorporate these traits into modern varieties. This will include the areas of plant nutrient acquisition, nutrient supply via soil microorganisms, and tolerance to soil-related biotic and abiotic stresses.

Have modern varieties lost genes associated with efficient direct and symbiotic nutrient acquisition?

Modern cultivar selection has typically been performed in standardized, high fertility soil conditions with a primary focus on yield. What consequence would this have on rhizosphere related traits? Under intensified agriculture, it is possible that crop selection undermined the capacity of some crops to access soil nutrients existing in forms not readily plant available. Furthermore, under such conditions, rhizosphere microbial communities are faced with an environment that differs substantially from the one in which plant–microbial interactions originally evolved (Drinkwater and Snapp 2007). Benefits incurred through interactions between plants and beneficial soil microorganisms may have been made obsolete by the excess provision of nutrients in readily plant available forms. Studies comparing allelic diversity within landraces and modern varieties tended to conclude that allele richness declined in modern varieties (Fu et al. 2005; Grau Nersting et al. 2006). It is likely that alleles contributing to beneficial plant–microbe interactions and associated with efficient nutrient acquisition strategies were among the alleles lost if such strategies incurred a cost to the plant and therefore compromised yield (Lambers et al. 2006).

Does that automatically imply that modern cultivars are nutrient inefficient? That depends largely on how nutrient efficiency is defined. If the definition is based on grain yield produced per amount of P applied or P contained in shoots, modern wheat (*Triticum aestivum* L.) cultivars tend to be equal to or more efficient compared to traditional varieties (Batten 1992). However, this is predominantly a function of their high harvest index and not some specific nutrient efficiency trait. Efficiency rankings typically reverse if P uptake or root efficiency (RE), the amount of P taken up per unit root size, is used to evaluate different germplasm and this was particularly apparent when no or very little P fertilizer was applied (Batten 1992; Wissuwa and Ae 2001).

In a screen of 30 diverse rice (*Oryza sativa* L.) genotypes on an Andosol containing a large pool of P fixed in forms of low plant availability, Wissuwa and Ae (2001) detected large genotypic differences in capacity to access P from this pool of soil-bound P (Fig. 1). Traditional varieties did not automatically show high P uptake ability but all genotypes capable of maintaining high relative P uptake were traditional varieties. It was interesting to note that the three genotypes with the highest root efficiency were all traditional upland cultivars from Japan that presumably were selected on similar soils. These results suggest that some traditional varieties possess specific adaptations to soils with low P availability. Similar conclusions were reached in other studies comparing the mycorrhizal competence of several wheat cultivars: those developed prior to 1950 were found to be more reliant on mycorrhizal symbiosis than modern

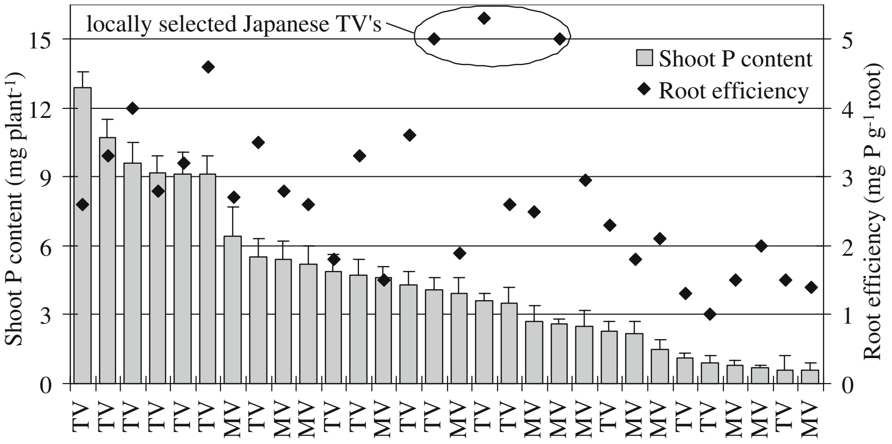

Fig. 1 Shoot P content and root efficiency (RE) of 30 rice genotypes of diverse origin and plant type. Depending on growth habit genotypes were classified as either (semidwarf) modern varieties (*MV*) or as tall traditional varieties (*TV*). Plants were grown under upland conditions in a highly P fixing soil (Andosol) that had never received P fertilizer. *Bars* represent standard errors of means (n=5; adapted from Wissuwa and Ae 2001; a more detailed description of genotypes used is provided in that paper)

wheat cultivars (Hetrick et al. 1992, 1993). Furthermore, landraces of mycorrhizal wheat grown in low-P soils produced a higher yield than modern varieties grown under the same conditions (Egle et al. 1989). This is in agreement with Zhu et al. (2001) who found that mycorrhizal responsiveness of modern wheat cultivars, measured in terms of shoot P, was generally lower than that of older cultivars. Such an observation has also been reported for plant associations with beneficial microorganisms other than mycorrhizal fungi. For example, root endophytes such as *Azoarcus* spp. or *Neotyphodium* and *Acremonium* preferentially colonized wild species and older varieties over modern cultivars of rice (Engelhard et al. 2000) and wheat (Marshall et al. 1999), respectively.

The reintroduction of genes regulating such adaptive traits into the genepool of modern varieties may represent the most promising means to improve their direct or symbiotic nutrient acquisition capacity (Ismail et al. 2007; Bosco et al. 2006).

Past efforts to breed for tolerance to abiotic and biotic stresses

Host plant resistance is an economically sustainable and environmentally sound measure for the management of abiotic and biotic plant stresses. Acid soils, and their associated toxicity (aluminum (Al) and manganese) and deficiency (P) syndromes (Kochian et al. 2004; Rao et al. 1993) are major constraints to crop production (von Uexküll and Mutert 1995). Thus, development of tolerant cultivars has received considerable attention, particularly since the 1980s (Magnavaca and Bahia Filho 1993; Rao et al. 1993; Sarkarung 1986). Local varieties with high aluminum tolerance existed for several crops but were of limited value due to various factors including low yield potential, poor grain quality and susceptibility to diseases and drought (Hede et al. 2001; Rao et al. 1993). Modern varieties, on the other hand, were not adapted to the acid soil syndrome, which meant the typical Green Revolution strategy in cultivar development could not be followed where soil acidity posed severe growth restrictions. Instead localized selection based on crosses between adapted genotypes and high-yielding cultivars seems to have been very common (Sarkarung 1986). Subsequent selection of adapted germplasm was typically done without liming and at low levels of N and P inputs (Rao et al. 1993; Sarkarung 1986). This strategy has produced improved cultivars of rice, wheat and maize (*Zea mays* L.) that combine tolerance to the acid soil syndrome with higher yield potential and tolerance to several important diseases (Hede et al. 2001; Magnavaca and Bahia Filho 1993; Rao et al. 1993).

Breeding for plant resistance towards foliar pathogens has been essential to the continued productivity of certain crops such as wheat (Line and Chen 1995) and rice (Wang et al. 2005; Zhai et al. 2002). However, with a few exceptions there has been an absence of similar programs addressing resistance or tolerance toward pathogens inciting diseases of the plant root system. Interestingly, the capacity for such efforts to yield benefit were inadvertently demonstrated, such as in the instance of tree fruit rootstock breeding programs focused on horticultural traits (Khanizadeh and Granger 1998), which unintentionally produced material with tolerance toward specific soilborne pathogens (Browne and Mircetich 1993). Mechanisms other than host resistance likely contribute to plant tolerance towards soilborne pathogens. It has been suggested that plants have evolved strategies of stimulating and supporting specific groups of antagonistic microorganisms in the rhizosphere (Cook 2006; Smith et al. 1999). Differential capacity of plant genotypes to support specific groups of resident as well as introduced microbial antagonists has been repeatedly reported (Berg et al. 2002; Larkin et al. 1993; Mazzola and Gu 2002; Mazzola et al. 2004). More importantly, a genetic basis for specialization between a microbial antagonist and a plant host has been demonstrated (Smith et al. 1997, 1999). A more comprehensive understanding of the impact of plant genotype on the non-symbiotic microbial community resident to the rhizosphere may have significant benefit to plant selection programs focused on development of disease tolerance/resistance.

Plant breeding for rhizosphere-related traits

The desire for more efficient utilization of resources in high input agriculture and enhanced adaptation to low fertility and other biotic and abiotic soil stresses in developing countries have already precipitated several changes in the conduct of plant breeding. Two key strategies currently being pursued are (1) broadening the genetic base of modern varieties through the reintroduction of genes from suitable donors such as traditional varieties or wild relatives (Ismail et al. 2007), and (2) selection of cultivars in systems employing no or reduced fertilizer and pesticide inputs (Bänziger et al. 1997). The problem remains that heterogeneous environments make it difficult to consistently apply high selection pressure to identify few superior genotypes across environments. Increasingly this is offset by highly decentralized selection in on-farm trials in unfavorable environments, which may involve farmer participation to select locally adapted and accepted material (Ceccarelli and Grando 2007; Dawson et al. 2007). In doing so breeders will inadvertently be selecting for beneficial rhizosphere related genes such as host genes affecting plant–microbe associations, or genes improving nutrient acquisition.

Useful traits of direct nutrient acquisition capacity and tolerance to abiotic soil stresses

The capacity of any genotype to acquire essential nutrients from the soil relies essentially on the two factors, (1) nutrient interception, which is dependent on root size and architecture, and (2) the acquisition process as affected by efficient uptake of available nutrients and solubilization or mineralization of less plant-available nutrients (Hinsinger et al. 2005; Ismail et al. 2007; Lambers et al. 2006). Plant–microbe interactions may play a role in both processes but will be discussed in following sections. Here the focus shall be on processes directly affected by plant adaptations.

Where low nutrient availability limits overall plant growth an increase in the root–shoot ratio has typically been observed as an adaptive response. This does not mean, however, that root growth is not reduced in absolute terms. In fact it has been shown for rice that the ability to maintain root growth is more closely linked to tolerance to P or zinc (Zn) deficiency than the non-stress root growth potential (Wissuwa and Ae 2001; Ismail et al. 2007). To understand what enables tolerant genotypes to maintain such high relative root growth rates will be a key factor in designing crops with improved nutrient acquisition capability (Lynch 2007). Through a modeling approach Wissuwa (2003) showed that small genotypic differences in factors improving P uptake per root biomass may provide enough extra P to maintain root growth with large subsequent effects on P uptake through improved root interception. From a physiological perspective, a focus should be placed on traits leading to enhanced root exudation of compounds capable of solubilizing soil-bound nutrients such as P (Lambers et al. 2006), Zn (Hoffland et al. 2006) or iron (Fe; Ishimaru et al. 2006). Enhancing the excretion of phosphatases or phytases to access organic P forms in soils appears less promising because of complex sorption/desorption characteristics in soil (George et al. 2004).

Several root structure related traits may also offer possibilities for improving nutrient acquisition. These include enhancing density or length of root hairs (Gahoonia and Nielsen 2004), modifications in root architecture to preferentially concentrate root biomass in soil strata containing the maximum amount of a limiting nutrient (Rubio et al. 2003), and ways to maintain new root development with minimal expenditure of additional resources either through more rapid root turnover (Lambers et al. 2006) or through etoilation (Lynch 2007).

Often nutrient deficiencies are due to interactions of multiple soil-related stresses. The acid soil syndrome is a good example as P deficiency is exacerbated by root growth reductions due to Al toxicity (Kochian et al. 2004). Similarly Zn deficiency can be aggravated by the negative effect high bicarbonate concentrations, typically encountered in alkaline/sodic soils, have on root growth in intolerant genotypes (Ismail et al. 2007). Therefore, in attempts to enhance nutrient acquisition capacity, one must take into account that interactions between several stress factors may occur in problem soils and that improvements in single traits may not be sufficient to improve genotype performance.

In selecting for improved nutrient efficiency under high-input systems, it is not clear whether nutrient acquisition or internal nutrient use efficiency plays a dominant role and therefore what traits would be beneficial. Maize lines with higher N efficiency have successfully been selected but their improved efficiency was apparently not due to better N uptake or any other rhizosphere trait (Paponov et al. 2005). In rice internal N use efficiency was also the more stable and therefore more selectable trait but genotypic differences in N uptake were also reported (Tirol-Padre et al. 1996). A more clear argument for the importance of rhizosphere traits in the uptake of nutrients in sustainable but highly productive agricultural systems can probably be made for nutrients such as P and Zn that are easily sorbed onto soil surfaces and hence show low mobility in soils (Singh et al. 2005). For both nutrients, traits discussed above for deficient conditions should also be beneficial under mild deficiency.

Useful traits for better nutrition via beneficial plant–microbe interactions

Harnessing the potential of beneficial plant–microbe interactions to manage nutrition (and diseases) in agroecosystems can be considered as an alternative, or a supplementary means, for reducing the use of chemicals in agriculture (Rengel and Marschner 2005; Picard and Bosco 2008). Managing these beneficial plant–microbe interactions can be achieved through various agricultural practices, such as the selection of the appropriate host plant species or cultivar, the degree and type of fertilization and crop rotation or soil tillage (Mazzola and Gu 2002; Oehl et al. 2004; Sarniguet et al. 1992), and in some cases by inoculations. Concerning the plant-genotype selection approach, the first step should be aimed at evaluating genetic variability of the crop plant. This phase should be devoted to the screening of plant genotypes available for selection (genetic resources) and characterization of beneficial microbial populations in the rhizosphere of such genotypes (Tanksley and McCouch 1997). These evaluations should be performed in low-input environments in order to reveal optimal plant–microbial interactions in limiting environments.

Host variation in responsiveness to beneficial microorganisms generally has been expressed as microbial root-colonization density and diversity, as well as effective plant growth stimulation. A major challenge in screening for enhanced microbial root-colonization is the design of effective procedures that provide a reproducible classification in the field environment. Level of root colonization exhibits dramatic variation related to plant age (Picard et al. 2000, 2004; Roesh et al. 2006), thus genotype rank can vary significantly depending upon plant age at the time of analysis. For example, the frequency of beneficial root-colonizing microorganisms was found to be very low in the initial stage of plant growth, greatly increased at the flowering stage, and then decreased with physiological maturation, at least for maize (Picard et al. 2000, 2004, Roesh et al. 2006) and for *Achillea ageratum* L plants (Picard and Bosco 2003). Interestingly, it is also at the flowering stage that greater differences in root colonization are observed between maize cultivars (Picard and Bosco 2005, 2006; Picard et al. 2004, 2008). Therefore, for maize and *Achillea ageratum* L, it is recommended that screening of plant-genotypes for the ability to support rhizosphere colonization by beneficial microorganisms be conducted at the flowering stage.

Independent of the beneficial association studied, it has been established that host genotype has a substantial impact in determining the extent of microbial colonization. For example, diversity in mycorrhizal responsiveness, defined in terms of mycorrhizal dependency (Tawaraya 2003) was observed among wheat genotypes by Hetrick et al. (1992, 1995, 1996). Interestingly, it was reported that diversity in capacity of wheat to sustain root colonization by mycorrhizal fungi was associated with yield responses, varying from zero to positive or negative values (Xavier and Germida 1998). Furthermore, mycorrhizal dependency is often negatively correlated with root morphological traits, such as root length, root dry weight, root hair length and density of root hairs, traits known to improve the ability of the non-mycorrhizal plant to acquire P directly from soil (reviewed in Tawaraya 2003).

Concerning atmospheric N_2 fixation, root nitrogenase activity and quantification of plant N derived from the atmosphere (Ndfa) have also been taken into consideration, both for rhizobial–legume symbiosis and plant associations with free-living microorganisms. Specifically for legumes, number of nodules was a quantitative trait measured to assess host reaction. Significant genotypic variation in the responsiveness of legume cultivars to *Rhizobium* has been reported. A range of bean (*Phaseolus vulgaris* L.; Hungria and Phillips 1993), soybean [*Glycine max* (L.) Merr.; Cregan 1989] and Lucerne (*Medicago sativa* L.; Hungria and Phillips 1993) genotypes differed in relative nodulation. Furthermore, high variability in N_2 fixation was observed among crop legume genotypes, varying from 0% to 97% (in percentage of crop N derived from N_2 fixation; see Herridge and Rose 2000). Differential capacity to support associative N_2 fixation has been clearly established among cereal species as well as among genotypes within cereal species (Jagnow 1990). Maximal nitrogenase activity was reported to be dependent upon maize genotype

(Ela et al. 1982; Neyra and Dobereiner 1977). Furthermore, Picard et al. (2008) recently gave clear evidence that maize genotype influences the size of microbial communities involved in N_2 fixation, as well as the diversity of the mycorrhizal fungi colonizing population. App et al. (1986) indicated for the first time that rice lines differentially influence beneficial N_2 fixers. By comparing 69 rice lines from diverse backgrounds (indica, japonica, and javonica; traditional and improved) and from different maturity groups (early, medium, and long), Shrestha and Ladha (1996) demonstrated that Ndfa differed significantly amongst the various lines, ranging from 1.3 to 20%. Those with high Ndfa were mostly traditional varieties, but some improved lines also had high associative N_2 fixation. Furthermore, appropriate combinations of *Acetobacter diazotrophicus* and rice genotype are needed for the relationship to be effective: some plants grew for up to 12 months on N-free medium obtaining N from the associative fixation (Rolfe et al. 1997).

Interestingly, these cultivar-dependent variations in interactions with beneficial microorganisms seem to have resulted from evolution over generations (Engelhard et al. 2000). In most cases, the capacity of a plant-genotype to positively interact with beneficial microorganisms appears to be an inherited trait (Rengel 2002; Smith and Goodman 1999).

Useful traits for a better barrier to pathogen infection of plant root

Although soil type has a considerable influence on the structure of microbial populations (Dalmastri et al. 1999; Latour et al. 1996; Marschner et al. 2001), plant species and genotype also are significant factors determining composition of microbial communities resident to soils and the rhizosphere (Berg et al. 2002; Dalmastri et al. 1999; Lemanceau et al. 1995; Marschner et al. 2001; Mazzola and Gu 2002; Miethling et al. 2000). As microbial populations indigenous to the rhizosphere can be considered an initial barrier to pathogen infection of plant roots, active manipulation of this community may be an effective means to suppress soilborne plant pathogens. The evolving view is that a degree of host specificity exists in interactions between plants and microbial antagonists (da Mota et al. 2002; Mazzola and Gu 2002; Notz et al. 2001; Smith et al. 1999), both those introduced as potential biological control agents and those that are resident to the soil ecosystem. Although the vast majority of studies have focused on the saprophytic bacterial community as the source of antagonists, there is also evidence to indicate that plant species differentially support root colonization by fungi, such as *Trichoderma*, *Penicillium*, and non-pathogenic *Fusarium* spp., with potential to suppress plant pathogens (Berg et al. 2005; Larkin et al. 1996; Rengel and Marschner 2005). Thus, utilization of crop genotypes with an elevated capacity to select for specific functional microbial genotypes would appear to be a viable means to enhance crop disease tolerance/resistance and ultimately productivity. However, as acceptance of this phenomenon as a valuable parameter to crop improvement is still considered novel, there exists a lack of breeding effort in this realm.

Although the body of work consists primarily of studies conducted in controlled environments, plant genotype-dependent selection of specific resident soil microorganisms having a functional role in disease suppression has been reported. The vast majority of work addressing the impact of plant genotype on selection of microbial antagonists has focused on fluorescent *Pseudomonas* spp. strains producing the antibiotic 2,4-diacetylphloroglucinol (2,4-DAPG) which has activity toward numerous soilborne plant pathogens (Keel et al. 1992), including take-all of wheat. Wheat genotypes were found to differentially support populations of an introduced 2,4-DAPG-producing strain (Mazzola et al. 2004) and varied in the capacity to selectively enhance resident populations of these bacteria when soils were cropped to successive wheat plantings (Fig. 2). Such a finding is of significance as development of take-all suppressive soils in response to continuous wheat monoculture results from an enrichment in populations of 2,4-DAPG-producing *Pseudomonas fluorescens* to a density of 10^5 CFU/g of root, the threshold required to suppress the causal pathogen, *Gaeumannomyces graminis* var. *tritici* (Raaijmakers et al. 1999). Likewise, qualitative attributes of the 2,4-DAPG-producing bacterial genotype recovered from the rhizosphere also varied with plant genotype (Mazzola et al. 2004) and age (Picard et al. 2000). Individual wheat cultivars selected for distinct dominant 2,4-DAPG genotypes from the same soil microbial community and the genetic diversity of the population

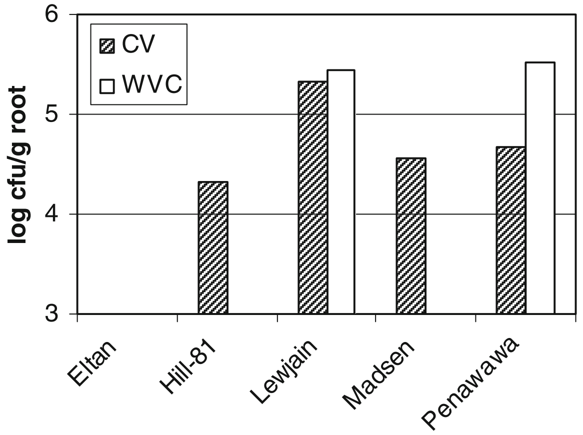

Fig. 2 Recovery of 2,4-DAPG-producing fluorescent pseudomonads from the rhizosphere of five wheat genotypes grown in Columbia View (*CV*) and Wenatchee Valley College (*WVC*) orchard soils. The limit of detection was 10^4 cfu g^{-1} root and indigenous populations of these bacteria were not recovered from the rhizosphere of cv. Eltan when grown in either soil, nor the rhizosphere of cv Hill-81 or Madsen grown in WVC soil. For a given soil, *values designated with the same letter* are not significantly ($P>0.05$) different (Mazzola et al. 2004)

recovered from the maize rhizosphere was related to plant age. Certain 2,4-DAPG-producing genotypes are known to possess superior disease control potential in part due to superior colonization abilities (Raaijmakers and Weller 2001).

Plants may also have direct impact on regulation of microbial genetic elements directly conferring activity of introduced biological control agents, thereby affecting disease control efficacy. Significant differences in expression of the 2,4-DAPG biosynthetic gene *phlA* were detected in the rhizosphere of different plant species with greater expression in the rhizosphere of monocots than in the rhizosphere of dicot species (Notz et al. 2001). Plant genotype effect on *phlA* expression was also observed within species, with significant differences detected among six maize cultivars. Similarly, Okubara (2006) determined that wheat cultivars differed in the ability to sustain root populations of these bacteria and to accumulate 2,4-DAPG in the rhizosphere.

Perhaps the most persuasive finding that could motivate the breeding of plant materials specifically for the capacity to modulate resident soil microbial populations in a manner that yields effective disease control is the observation that soil suppressiveness is induced in a plant genotype dependent manner. Larkin et al. (1993) documented the development of *Fusarium* wilt suppressive soils in response to repeated cultivation of soil with watermelon [*Citrullus lanatus* (Thunb.) Matsum & Nakai]. This response was only observed when cultivars resistant to *Fusarium oxysporum* f. sp. *niveum* were employed, and was associated with increases in specific populations of non-pathogenic *Fusarium oxysporum*, with many of the isolates possessing the capacity to induce host systemic resistance (Larkin et al. 1996). Soil suppressiveness toward Rhizoctonia root rot in response to repeated cultivation of wheat was also found to occur in a wheat genotype dependent manner (Mazzola and Gu 2002). Capacity of a wheat genotype to induce disease suppression was associated with enhancing rhizosphere populations of specific fluorescent pseudomonad genotypes demonstrating antagonistic activity toward *Rhizoctonia solani* AG-5 and AG-8 (Gu and Mazzola 2003). Cultivation of wheat genotypes that did not modify the fluorescent pseudomonad population in this manner did not elicit a disease suppressive soil.

Rhizosphere-related breeding: current approaches

Several approaches are being followed to introduce beneficial rhizosphere traits into modern varieties. At present, most involve modifications in conventional breeding strategies but with the rapid advances being made in molecular techniques they will increasingly rely on alternative breeding strategies such as marker assisted selection or genetic modifications. This section will discuss the recent changes in breeding approaches.

Changes in conventional approaches—indirect selection

As a result of difficulty in assessing rhizosphere related traits in breeding programs that typically evaluate thousands of segregating progeny, selection for beneficial rhizosphere traits is typically carried out indirectly, e.g. by selecting for yield in an environment where a particular rhizosphere related trait should confer an advantage. To assure that such indirect selection actually exposes benefits of rhizosphere traits the following strategies have been employed:

1. Choice of donors to complement modern varieties in traits that are so far missing

2. Subsequent selection conducted in environments that should favor progeny with introgression of beneficial traits
3. Participatory plant breeding

Choice of donors to complement modern varieties

The selection of donors with a highly favorable phenotype for a trait of interest has been the most commonly used strategy in improving plant adaptation to edaphic factors in the past and can therefore not be called a novel approach. However, as our understanding of the complexity of plant–soil interactions increases, criteria for the selection of donors continue to evolve and include novel traits such as root shallowness as measured by root growth angle in bean or soybean seedlings (Lynch 2007), root hair length (Gahoonia and Nielsen 2004) or adventitious root number (Ochoa et al. 2006), all traits associated with improved P uptake.

The identification of germplasm with resistance to pathogens has had a prominent role in the historical control of plant pathogens. The development and use of resistant cultivars has been effective in controlling *Fusarium* wilt of numerous crop plants caused by the ubiquitous and specialized fungal pathogen *Fusarium oxysporum* (El Mohtar et al. 2007; Herman and Perl-Treves 2007).

Although the effectiveness of such a strategy for the management of less specialized root pathogens, such as *Pythium* and *Rhizoctonia* spp. has been questioned (Cook et al. 1995; Cook 2006), certain reports suggest that some useful measure of tolerance is attainable. However, the sources are commonly wild plant populations and will require transfer to commercially relevant plant genotypes. Novel sources of resistance to *Rhizoctonia solani* were identified in a screening of wild *Beta* germplasm (Luterbacher et al. 2005) and polygenic resistance to Rhizoctonia root rot was identified in sugar beet (*Beta vulgaris* L.; Panella 1998). Evaluation of 16 apple (*Malus domestica* Borkh.) genotypes, representing commercially available rootstocks as well as developmental material from an apple-rootstock breeding program (Fazio and Mazzola 2005) documented wide variation in susceptibility to root infection by *Rhizoctonia solani* AG-5, with infection rates ranging from 6 to 65%. Furthermore, the wild apple *Malus sieversii* is highly resistant to this fungal pathogen, and crosses between this resistant wild material and Geneva dwarfing elite rootstocks has yielded resistant genotypes (Fazio et al. 2006). Differential susceptibility to indigenous populations of *Pythium* spp. was also detected, with Geneva rootstocks in general less susceptible to infection than those of the Malling series. Resistance to pre-emergence damping off incited by *Pythium* spp. has been reported for several crops including soybean (Kirkpatrick et al. 2006) and subterranean clover (*Trifolium subterraneum*; You et al. 2005). However, in screening of a subterranean clover breeding line, there was no association between resistance to pre-emergence damping-off incited by *Pythium irregulare* and root rot caused by this same pathogen. Among 50 lines tested, a single line exhibited resistance to root rot incited by *P. irregulare.*

Selection in environments that favor progeny with introgression of beneficial traits

Following the introgression of beneficial traits from donors into a segregating breeding population it is crucial to conduct selection among progeny in environments that expose advantages of such introgression. This represents a deviation from the classical breeding approach so successfully employed in the development of the highly productive Green Revolution varieties. The advantage of selection in high-input environments has led breeders to assume that a carry-over effect of high yield potential into unfavorable environments can be realized. However, experimental evidence suggests that this is not necessarily the case and that unfavorable environments are frequently below the cross-over point at which genotypic rankings in response to environment are reversed (Ceccarelli and Grando 2007). Rather than reducing the impact of environment on genotype performance through fertilization, soil amendments or disease control, genotype x environment effects therefore need to be exposed and selected for under low input conditions and with the presence of biotic and abiotic soil stresses.

One of the first breeding programs targeting low input environments was the upland rice breeding program at CIAT, Colombia. Initiated in 1982, emphasis was first placed on identifying donor genotypes among a broad collection of landrace and improved upland varieties in screening experiments conducted on acid soils with low fertility (Rao et al. 1993). Subsequent 'decentralized' selection in segregating populations was done under a range of soil fertilities to identify lines that showed both improved yield potential in low-fertility conditions and high yield potential in more favorable environments. As a result several new rice cultivars have been released, emphasizing benefits of decentralized selection over a range of target environments. A similar yet more targeted approach, as donors were selected for their favorable expression of root anatomical traits, is currently being followed in developing bean, maize and soybean cultivars with adaptation to low P availability (Lynch 2007; Yan et al. 2006).

A similar approach was utilized in the selection of sugarcane (*Saccharum officinarum* L.) varieties in Brazil in which breeding programs used both local and introduced material and were conducted in the absence of large N inputs. This method has led to Brazilian sugarcane varieties that are able to incorporate up to 70% of their total N from associative bacterial N_2 fixation (Andrews et al. 2003; Baldani et al. 2002). This may be the reason why today the best materials have little demand for N fertilizer, and an effective association has developed between endophytic N_2-fixing bacteria and the plant (Baldani et al. 2002).

Breeding programs for enhancing N_2 fixation in legumes have had particular application to cropping systems encountered in unfavorable environments of developing countries. One of these successful legume breeding programs is that of Bliss, which over a period of 13 years made substantial progress in selecting for yield of common bean in low N soils. This work resulted in the release of five high N_2 fixing lines well adapted to the South America (Bliss 1993). A second example is the soybean breeding program realized in Africa by the International Institute of Tropical Agriculture (IITA). In this case, soybean genotypes nodulated by indigenous rhizobia and demonstrating an acceptable yield were successfully selected among the locally used cultivars (Nangju 1980).

Selection in most breeding programs for maize, based on the phenomenon of heterosis, has resulted in superior modern maize hybrids that produce yields that range from 150% to over 300% of their parental mean (Hallauer and Miranda 1988; Shull 1908). Interestingly, by comparing populations of plant-beneficial microorganisms isolated from maize hybrids and from their respective parental lines, it was shown that microbial root colonization could be related to heterosis (Picard and Bosco 2005, 2006; Picard et al. 2004). Repeated field experiments demonstrated that maize hybrids are more abundantly colonized by beneficial bacterial strains with greater genetic differences and more effective in disease suppression, root stimulation and associative N_2 fixation, than those supported by their respective parental lines. Similar results were also obtained for mycorrhizal symbiosis (Picard et al. 2008). These findings suggest that, in this particular instance, the conventional breeding programs for maize based on heterozygosis have inadvertently selected for maize genotypes able to support large and genetically diverse populations of efficient plant beneficial microorganisms.

Establishing environments suitable for the effective evaluation of host resistance to soilborne plant pathogens is not a trivial undertaking. Disease severity is a product of numerous interactions among the resident soil biota in addition to the general nutritional status of the plant. For diseases of complex disease etiology, attending to one biological issue is likely to elevate the impact of another component as often the contributors are direct competitors for a specific niche and once released from this competition may result in elevated damage levels (Mazzola 1998; Pieczarka and Abawi 1978). While addressing all such issues in the design of a specific environment for screening plant germplasm is not likely to be practical, addressing certain basic parameters will improve the validity of screening programs. Much like the limitations concerning the selection of cultivars in systems possessing unlimited nutrient availability, screening of crop material in the absence of any potential limits placed upon it through the activity of soil microbes can have unforeseen negative outcomes. Such may have been the case with regard to certain strawberry (*Fragaria* Duch.) breeding programs where selections were concluded based upon growth in fumigated soils, which yielded varieties that are highly susceptible to a wealth of soilborne pathogens. While the highly methyl bromide fumigation-dependent strawberry material from the California breeding system initially yielded no obvious genetic diversity for developing cultivars adapted to sublethal effects of organisms in non-fumigated soils (Shaw and Larson 1996), tolerance to black root rot, incited by a complex of non-lethal pathogens, was detected among three genotypes released from the breeding program in Nova Scotia, Canada (Particka and Hancock 2005).

While field level evaluations of host resistance are critical to the screening program, a common hurdle to the conduct of these trials is the absence of suitable disease pressure. A typical manner to circumvent this difficulty is to augment the target population by infestation with laboratory raised inoculum, which usually emanates from one or a few strains of the pathogen. In certain instances, this may be essential where resistance to a specific race or *formae specialis* of the pathogen is the subject of the breeding program. However, this has the possibility of generating a further limitation to the process by restricting plant exposure to the genetic diversity which exists in any pathogen population. For many soilborne pathogens, a straightforward means of enhancing indigenous inoculum is through cultivation of a susceptible host prior to establishment of the screening trial (Gutierrez and Cramer 2005). In actuality, some combination of controlled and field assessment is likely as a limit to the amount of material screened is often necessitated by field trial expenses.

Participatory plant breeding

Marginal environments are typically characterized by the concurrence of several stresses. When rainfall patterns vary from year to year, risk-averse farmers typically do not apply fertilizers or other costly inputs. Thus environmental stresses tend to be heterogeneous and site or region specific. Under such conditions the “on-station” approach of developing varieties with broad adaptation has had limited success (Ceccarelli 1994). A second limitation of the centralized approach to cultivar development is that attributes other than grain yield may determine whether cultivars are accepted locally (Morris and Bellon 2004). Such secondary attributes may involve specific grain quality traits or an emphasis on straw yield and suitability as animal feed.

To develop locally adapted and accepted varieties several participatory plant breeding strategies have been developed that involve farmers at various stages of the selection process (Ceccarelli and Grando 2007; Dawson et al. 2007). One such participatory plant breeding approach in which farmers evaluated progeny from several crosses in their own fields, yielded release of two rice varieties that showed particular advantages over a check variety under low input/low yield conditions while being inferior to the check in more productive environments (Virk et al. 2003). A slightly different approach is to let breeders conduct selection within their segregating material but to disseminate near-finished lines for farmer participatory variety evaluation, possibly conducted at farmer fields with little or no fertilizer inputs. A perceived advantage of this approach is testing in a large number of locations and rapid dissemination of farmer preferred seed at respective locations. Bänziger and Diallo (2001) summarized results from maize evaluation trials in low N/low rainfall environments and concluded that this participatory evaluation approach was very successful not only in developing adapted cultivars but importantly also in bringing them into farmer’s fields.

Direct selection for rhizosphere related traits

Direct selection for rhizosphere traits in segregating populations remains rare because of the potential high cost of evaluating hundreds if not thousands of lines. However, this additional cost can be justified if the heritability realized in direct evaluations is far greater than in indirect screens under field conditions. Yan et al. (2006) and Lynch (2007) suggested that rapid screens available for certain root morphology/architecture traits may actually be more cost-efficient than selection for yield in fields with high spatial soil heterogeneity. Root hair length and density is one example of a highly heritable trait (Gahoonia and Nielson 2004; Yan et al. 2004) that is currently being used successfully in selections among segregating populations of bean and soybean (J. P. Lynch, pers. comm.). Another example is the glasshouse screening method developed at CIAT to evaluate Al tolerance and root growth vigor in vegetative propagules of the forage grass *Brachiaria* (Ishitani et al. 2004).

However, it may be concluded that direct selection for rhizosphere traits remains an exception, either because few suitable traits have been identified to date or because the expression of such traits are prone to variation depending on growth stages or environmental conditions. Much could be gained if phenotypic evaluations are replaced by selection for molecular markers tightly linked with the trait of interest. Considerable effort has therefore been invested in mapping quantitative trait loci (QTLs) associated with rhizosphere traits.

Targeted introgression of rhizosphere traits via marker assisted selection (MAS)

Using tightly linked markers to indirectly select for a trait of interest should be ideally suited to transfer important rhizosphere traits to modern varieties because of the difficulties in evaluating and selecting for rhizosphere traits directly. Numerous studies have been conducted to map QTLs associated with rhizosphere traits, however, very few of these QTLs have been used in practical breeding programs. In reviewing factors responsible for the apparent lack of success in turning mapped QTLs into tools for plant breeding, Wissuwa (2005) concluded that the bottleneck does not lie in a scarcity of identified QTLs but possibly in a lack of relevant QTLs identified by screening procedures that convince breeders of their usefulness in target environments. One challenge therefore is to identify or at least confirm benefits of QTLs in target environments. Given that the spatial variability in field trials is inherently large for nutrient availability/toxicity traits, accurate phenotyping will represent an obstacle in mapping nutritional traits that should not be underestimated.

Furthermore, not all QTLs identified can automatically be considered useful in breeding. Frequently one parent used in mapping populations was chosen because it showed an unfavorable phenotype that contrasted well with a second parent that may not have been outstanding with regard to the trait studied. A locus capable of improving a rather poorly performing parent is not necessarily suited for improving breeding material that already shows the favorable phenotype to some degree. Breeders are more inclined to include novel alleles with large effects in their programs and these have in the past been detected in mapping populations that included a donor showing a very favorable phenotype as one of the parents (Mackill 2006).

For the practical application of a QTL in marker assisted breeding, QTL positions need to be known with higher precision than typically achieved in initial QTL mapping experiments (Yano et al. 2000). The resources required to achieve this may be several-fold higher compared to the initial QTL mapping experiment. One of the few traits for which mapping has progressed to a stage where marker assisted backcrossing is feasible is tolerance to P deficiency as conferred by the *Pup1* locus in rice (Wissuwa et al. 2002). The strategy followed by the International Rice Research Institute (IRRI) and collaborators is outlined in Fig. 3. Key factors for the advances made with *Pup1* were the choice of a highly tolerant donor genotype (Kasalath) in QTL mapping, subsequent confirmation of the QTL effect in a near isogenic line (NIL) background, reliance on phenotyping in the field, precision mapping based on secondary mapping populations derived from a backcross of the tolerant NIL to intolerant recurrent parent ‘Nipponbare’, and identification of suitable recipient varieties. The aim at present is to simultaneously transfer tolerance to P deficiency with higher rice blast resistance to upland varieties having high yield potential under non-stress conditions (Ismail et al. 2007). Once the gene at the *Pup1* locus is cloned, efforts will be directed towards identifying additional and possibly even stronger alleles at this locus by screening additional gene bank accessions for novel polymorphisms within the locus (allele mining).

Probably the most extensively and successfully mapped rhizosphere related trait is Al tolerance. Part of the success with Al tolerance is due to the simplicity of phenotyping for this particular trait and

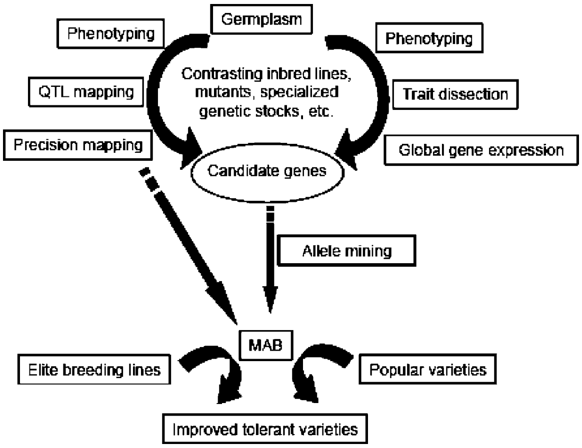

Fig. 3 Outline of a strategy for germplasm improvement for problem soils. Proper germplasm and genetic stalks were used for mapping traits associated with tolerance to salinity, P and Zn deficiency. The two major QTLs (*Saltol* and *Pup1*) were fine-mapped and QTL and gene-specific markers were identified and are being used in their introgression into elite breeding lines and popular varieties using marker assisted backcrossing (*MAB*). Genes in the two regions were also annotated, short-listed based on converging evidences from positional, functional and expression analysis and are being further validated (our unpublished data). Figure reproduced from Ismail et al. (2007) with kind permission of Springer Science and Business Media

the close correlation between nutrient solution screens and actual field tolerance. Furthermore, Al tolerance in several crop species [wheat, barley (*Hordeum vulgare* L.), sorghum (*Sorghum bicolor* (L.)) Moench] is in large part due to a single gene, subsequently found to be coding an aluminum-induced efflux transporter for malate (Sasaki et al. 2004) or citrate (Magalhaes et al. 2007; Wang et al. 2007). Based on these efforts marker assisted breeding is currently being practiced in sorghum breeding programs in Brazil (J. V. Magalhaes, pers. comm.).

Molecular biology, combined with Mendelian and quantitative genetics in quantitative trait locus (QTL) mapping and marker-assisted selection are more and more used for revealing the inheritance of root association with beneficial microorganisms. For example, it has been shown that interactions of maize with mycorrhizal fungi, or of rice with associative N_2 fixers, were associated with two and four QTLs, respectively (Kaeppler et al. 2000; Wu et al. 1995). Another interesting example is the case of the single nucleotide amplified polymorphism (SNAP) markers identified by Kim et al. (2005) for supernodulation in soybean. However, marker-assisted selection (MAS) for enhanced root-beneficial microbe association typically does not form a part of routine cultivar improvement programs, and incorporating selection criteria for such associations, such as nodule mass, N_2 fixation and responsiveness to mycorrhizal fungi, into breeding schemes while attending to other breeding objectives remains a challenge. If MAS for beneficial root-microbe interactions could be integrated into breeding programs that are already practicing MAS for other traits, this would avoid the necessity of additional phenotypic selection methodologies purely for determination of beneficial microbial-root associations.

Genetic determinants of resistance to *Fusarium oxysporum* for a specific host to the same formae specialis can vary, and in melon (*Cucumis melo* L.) has been reported to be monogenic and dominant, as well as conferred through polygenic effects depending upon the physiological race of the causal fungus, *F. oxysporum* f. sp. *melonis*, and the cultivar examined (Herman and Perl-Treves 2007). Similar differences in the genetic governance of wilt resistance has been described in chickpea (*Cicer arietinum* L.), with monogenic resistance described toward certain races of *F. oxysporum* f. sp. *ciceris* and oligogenic resistance toward others (Sharma and Muehlbauer 2007). Analysis of a recombinant inbred line population of melon possessing polygenic resistance to *F. oxysporum* f. sp. *melonis* resulted in the resolution of nine qualitative trait loci (Perchepied et al. 2005), and QTL for Fusarium wilt resistance have been identified in a number of other plant hosts (Iruela et al. 2007).

In tomato (*Solanum lycopersicum* var. *lycopersicum* L.), the *I-2* resistance gene for resistance to *F. oxysporum* f. sp. *lycopersici* Race 2 was mapped (Segal et al. 1992; Ori et al. 1997) and sequenced. Primers specific to the *I-2* gene were designed (El Mohtar et al. 2007) and used to screen a series of tomato varieties, with the expected amplicon only detected in varieties known to possess the *I-2* gene. When used to screen an uncharacterized F2 seedling population, the *I-2* gene was detected in 72 seedlings, 69 of 72 seedlings showed resistance to the pathogen, and among those lacking the resistance gene based on the PCR assay, 26 of 29 exhibited susceptibility. This method could be effectively employed in breeding programs to detect the presence of the *I-2* gene.

Introduction of new traits and genes through genetic modifications

Rapid developments in the field of plant molecular biology have accelerated the rate of gene discovery and promise to provide scientists and breeders with new genes of potential importance for the improvement of plant adaptation to unfavorable soil environments. Initial attempts to improve nutrient acquisition through overexpression of candidate genes have, however, yielded mixed results.

Transgenic *Trifolium subterraneum* transformed with a phytase gene from *Aspergillus niger* improved P uptake of plants supplied with phytate and grown in agar under sterile conditions (Richardson et al. 2001), but this positive effect was not seen in soil grown plants, possibly because phytate was bound to soil particles and therefore not available (George et al. 2005). Delhaize et al. (2001) overexpressed a citrate synthase gene from *Pseudomonas aeruginosa* in tobacco (*Nicotiana tabacum* L.) and detected greatly enhanced citrate synthase protein levels in the transgenic plants. However, neither citrate accumulation nor efflux was enhanced and consequently no positive effect on tolerance to Al toxicity was observed in transgenic lines. However, expressing a malate efflux transporter gene from wheat in barley did significantly improve aluminum tolerance in the transgenic barley lines (Delhaize et al. 2004).

A more robust approach may therefore be the transfer of genes known to confer tolerance to edaphic stresses from highly tolerant plant species to other species lacking certain components of tolerance mechanisms. The work of Nishizawa and coworkers has eloquently shown merits of this approach. Rice has evolved under flooded conditions characterized by high concentrations of Fe^{2+} in the soil solution. The adaptation to such high Fe^{2+} environments may have selected for an Fe uptake system predominantly relying on direct uptake of Fe^{2+} via the Fe^{2+} transporter OsIRT1 without a need to first reduce Fe^{3+} to Fe^{2+} (through Fe^{3+} chelate reductase) as would be required for other Strategy I species that rely on the IRT transport pathway and that evolved on non-flooded soils that predominantly contain the oxidized Fe^{3+} form. When grown in such aerobic soils rice is prone to suffer from Fe deficiency because of low Fe^{3+} chelate reductase activity and because of low phytosiderophore secretion compared to other graminaceous strategy II species like barley or wheat (Ishimaru et al. 2007). Nishizawa and coworkers followed two independent approaches to engineer rice plants with high tolerance to Fe deficiency. The first approach involved strengthening the Strategy II system by expressing two barley nicotianamine aminotransferase genes in rice. Transgenic rice plants secreted much larger amounts of phytosiderophores resulting in better performance in calcareous soils (Takahashi et al. 2001). The second approach was to reconstitute the first step of the Strategy I uptake system by introducing a Fe^{3+} chelate reductase gene from yeast fused to the Fe-regulated OsIRT1 promoter (Ishimaru et al. 2007). Transgenic rice plants had eight times higher grain yield compared to non-transformed plants when grown on calcareous soil. First field trials on calcareous soils confirmed experimental results even though yield benefits were lower than seen in pot experiments (Suzuki et al. 2008).

Future transgenic approaches will increasingly rely on using alleles from tolerant genotypes for transformation within a given species. At present this approach is limited by the low number of useful naturally occurring alleles identified. However, with sequence data available for an increasing number of relevant crop species and concerted international efforts directed towards allele mining (Generation Challenge Program 2007), progress will be made in the coming years. The identification of a major Al tolerance gene in sorghum through positional cloning of the *Alt_{SB}* locus is one of the most promising cases being actively pursued at the moment (Magalhaes et al. 2007). Several allelic variants of the Alt_{SB} gene have been identified from different donors and efforts are under way to identify the most effective allele, both through transgenic approaches and through marker assisted backcrossing (Caniato et al. 2007).

A similar strategy based on the identification of superior alleles via QTL mapping has led to the identification of several putative candidate genes at the Pup1 locus in rice (Ismail et al. 2007). NILs carrying the tolerance allele at the Pup1 locus showed threefold higher P uptake and grain yield in field trials conducted on a highly P deficient Andosol. Currently transgenic plants are produced for several candidate genes in an attempt to clone and characterize the responsible gene. A different approach based on screening for genes induced by P starvation led to the molecular cloning of the OsPTF1 gene in rice (Yi et al. 2005). OsPTF1 is a transcription factor that enhances root growth under P deficiency. Transgenic rice plants overexpressing the OsPTF1 gene showed 20% higher P uptake and biomass accumulation when grown in P deficient soil.

The development of transgenic resistance through molecular breeding programs may be central to the generation of plant genotypes suitably resistant to non-specific root pathogens. Attempts to confer resistance to *Rhizoctonia solani* have focused on the transfer of hydrolytic enzymes including chitinases (Broglie et al. 1991; Sareena et al. 2006) and glucanases capable of degrading cell walls of invading fungal pathogens to susceptible crop plants. While a modest level of resistance to foliar blight diseases caused by *R. solani* has been obtained (Datta et al. 2001), similar effort yielded minimal improvement in resistance to root rot disease incited by this pathogen. Transfer of the thaumatin gene from *Thaumatococcus daniellii* into tobacco delayed disease development incited by *R. solani* and *Pythium aphanidermatum* (Rajam et al. 2007). However, in the vast majority of instances trials assessing the conference of resistance have been conducted using extremely artificial systems or have considered disease development only in the seedling stage of plant development (damping-off) and have not assessed impacts on root rot diseases incited by these pathogens.

RNA interference technology is a phenomenon of gene silencing at the mRNA level that is a powerful research tool used in functional genomics. RNAi is being used to create plants having novel traits, including resistance to plant pathogens and parasites. In this realm initial efforts to develop resistance to diseases focused particularly on those caused by viruses. Recently, certain efforts have examined the utility of RNAi for the control of plant root parasitic nematodes, and most specifically the obligate sedentary endoparasites belonging to the genera *Globodera, Heterodera* and *Meloidogyne* (Lilley et al. 2007). Studies demonstrated that an RNAi like response could be achieved when artificially exposed to dsRNA (Urwin et al. 2002). Fewer nematodes were recovered from plants inoculated with pre-parasitic juvenile forms that had ingested dsRNA *in vitro* than plants inoculated with non-treated control nematodes. Subsequent studies in transgenic Arabidopsis [*Arabidopsis thaliana* (L.) Heynh.] and tobacco demonstrated that *Meloidogyne* could acquire plant derived dsRNA through root feeding activities (Fairbairn et al. 2007; Huang et al. 2006). In vitro ingestion of dsRNA of the parasitism gene *16D10*, which encodes for a parasitism peptide secreted by second stage juveniles, silenced the target gene in J2 juveniles of *M. incognita*. Reproduction of four *Meloidogyne* species was dramatically reduced on transgenic Arabidopsis expressing *16D10* dsRNA. The breadth of efficacy realized in *16D10* dsRNA expressing plants across species of *Meloidogyne* has not been realized in response to known resistance genes.

One difficulty associated with the transgenic approach in terms of making the leap from experimental verification to practical breeding is the lack of acceptance by a public skeptical of gene transfers, particularly if this involves different species. In this regard the transfer of useful alleles within a species should be less problematic and from this standpoint alone, more effort should be directed towards the identification of such useful alleles. A different approach that might be more acceptable is the generation of new allelic variation within species through mutagenesis. One example is that of Picard et al. (2007), who selected from 10 mutant lines belonging to a tomato (cv *Red Setter*) ethylmethane sulphonate (EMS) mutant collection, those possessing both good mycorrhizal competence and high productivity in order to obtain tomato genotypes adapted to low-input cropping systems. It is important to note that EMS mutations did not induce loss in fruit quality, since no relevant differences were observed between mutants and the isogenic line. In contrast, differences in the arbuscular mycorrhizal fungi (AMF) infection dynamics were observed between lines. Some differences were also found in the diversity of root-colonizing AMF taxa and in fruit quality. These differences in values for mycorrhization level, root infection dynamics, AMF population structure and fruit quality have been used to classify these mutants. Interestingly, results of this classification by these four characters tended to correlate. One tomato mutant was especially mycorrhizal-competent, showed a highly structured AMF population, and was highly productive. This mutant is the most promising culture for low-input cropping systems. Another example is the 15 EMS-induced mutants obtained by Carrol et al. (1985) from the parental Bragg soybean, which formed up to 40 times the number of nodules as the parent and continued acetylene reduction (N_2 fixation) activity.

Outlook: opportunities and limitations

It is obvious that there is a strong demand for plant breeding to produce new cultivars with improved yield potentials for application in low-input less favorable crop production environments. From the review of recent literature, it appears that it may be difficult to select cultivars for lower-input agriculture from the elite cultivars currently used in conventional agriculture. It has been broadly recognized that desirable traits will need to be reintroduced into elite cultivars and considerable effort has been devoted to the identification of beneficial traits and suitable donors for that purpose. Yet progress has been slow and has so far largely been confined to modifications of traditional breeding procedures such as decentralized selection under low input conditions. This is in stark contrast to the explosion of knowledge generated in plant sciences during the past decade. Based on the review of potentially useful traits in this paper and by others in this volume it is obvious that there is no shortage of ideas. How to turn these ideas into better varieties remains a critical and often unresolved question.

Several successful cases have shown that concepts do work in principle. Insights into plant adaptation to nutrient scarcity have identified traits that are being used in direct selection, for example root morphology in beans and soybeans (J. P. Lynch, pers. comm.) and symbiotic N_2 fixation in common bean (Bliss 1993). QTL mapping can lead to identification of new and useful alleles, such as those at the Alt_{SB} or Pup1 loci that are being used in MAS. Transgenic approaches did show their efficacy in improving tolerance even under field conditions (e.g. improving tolerance of Fe deficiency in rice; Suzuki et al. 2008).

However, given the large number of traits studied and that numerous QTLs have been mapped, it is surprising how few examples do find their way into practical breeding. Several factors, both political and scientific, may be responsible for this obvious gap between basic research and applied breeding. The success of the Green Revolution has up to very recently resulted in a food surplus and that has precipitated a shift in focus away from food security, particularly in highly developed countries. Consequently, investments in public research were predominantly channeled into basic research dominated by model systems such as *Arabidopsis thaliana*. Breeding on the other hand has increasingly been done by the private sector with a natural focus on high value seeds but not on poor people's varieties or crops. With funding and esteem being progressively more associated with basic research, training at universities has also shifted away from breeding and that may have further widened the gap between basic research and applied sciences. These economic and political changes in combination with the entirely new opportunities offered by ever-evolving molecular tools may be responsible for the shift in research focus away from complex systems such as plant–soil interactions to single gene/traits under highly artificial conditions.

Yet in order to bring novel approaches generated in basic science to applied plant breeding it will be crucial to narrow the gap between the two disciplines. In certain instances this has been recognized by public funding sources that have moved away from supporting model system research to specifically focus on research systems directly applicable to crop plants. The few success stories (breeding for enhanced Al tolerance, improved P acquisition) involved close collaboration between breeders and scientists conducting basic research and, by periodically testing material under field conditions, they did not avoid the complexity of plant–soil interactions. While stating the need for more interdisciplinary and field-based research may appear mundane, it seems obvious that the lack of such approaches has resulted in a significant impediment to making further progress through plant breeding, especially with regard to materials of value to low-input "sustainable" systems. We therefore want to put forward a few points that we believe are key to making progress in this regard:

- Phenotypes need to be confirmed under realistic field conditions in order to establish that traits warrant attention in breeding programs. Such a 'reality check' is also of benefit for basic research because it assures that mechanisms studied or genes identified are practically relevant.
- Rapid screening protocols that correlate closely to field performance are essential for applied breeding and considerable effort should be directed towards their development.
- It is important to realize that allelic variation, as detected in QTL mapping studies, is not equal to useful allelic variation. Without confirmation of QTL effects in NIL backgrounds, QTL mapping will remain a purely academic exercise. Only strong alleles that can significantly improve a phenotype will find their way into breeding programs.
- Similarly, genes identified in unsystematic reverse genetic screens may be of little practical use. More effort should be directed towards identification of superior phenotypes and their underlying genes.
- Finally a more holistic view will be needed that takes into account the trade-offs or synergistic effects existing for many traits.

Employing such a holistic view will eventually enable us to redesign plants by pyramiding of genes or QTLs in order to combine traits or genes to enhance processes that need simultaneous activity of several components. An ideal new variety would show enhanced root interactions with beneficial microorganisms (mycorrhizal fungi and rhizobacteria), soilborne disease resistance and/or nutrient acquisition capability and tolerance to abiotic soil stresses. For the case of improved capability to access soil-bound P, plants of the future would present high affinity with mycorrhizal fungi (Bosco et al. 2006; Rengel 2002), or would show enhanced carboxylate exudation to release inorganic as well as organic P sources into the soil solution (Gahoonia and Nielson 2004); they should furthermore have higher phytase/phosphatase excretion rates to break down the organic P forms and this would be combined with increased root hair length to facilitate exudation and uptake at larger distances from the root surface. All of these traits have so far been studied in isolation and with limited success in terms of producing the desired phenotype (Delhaize et al. 2001; Richardson et al. 2001). The more difficult task of combining them in a single genotype awaits realization.

With further advances in molecular techniques and in our understanding of which genes govern highly complex traits ever more possibilities for engineering crops will arise in the future. Turning cereals into efficient N_2 fixing crops or reducing N losses through enhancing the release of natural nitrification inhibitors by crops (Subbarao et al. 2007) may be feasible one day. However, in the meantime non-renewable resources are being diminished and poverty in rural areas of developing countries remains extremely high. Improved varieties are therefore needed urgently and more effort to combat present problems with present technological means is warranted. Further emphasis on bridging the gap between breeding and basic sciences is therefore needed from policy makers, science managers, funding agencies and, ultimately from the scientists involved. It is encouraging to see that this is successfully done in research organizations of Brazil, China, Australia, and in the research centers belonging to the Consultative Group on International Agricultural Research (CGIAR); however, much could be gained if such a shift in emphasis were realized in some of the most developed countries as well.

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