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Root Traits and Rhizosphere Characteristics Determining Potassium Acquisition from Soils

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Abstract

Plants acquire K^+ ions from the soil solution, and this small and dynamic pool needs to be quickly replenished by the other soil pools, either the exchangeable pool via desorption of K adsorbed onto clay minerals and organic matter, or the nonexchangeable pool via weathering of K-bearing silicates. Because of these chemical interactions with soil solid phases, K^+ concentration is kept low, restricting its mobility. Mass-flow therefore only partly contributes to K^+ transfer to the root surface, and K^+ depletion occurs as a consequence of K^+ uptake by roots, which is the driving force for the diffusion of K^+ in the rhizosphere. Because of this restricted mobility of K in soils, plants have evolved efficient strategies of root foraging. Therefore, root traits related to root system architecture (root angle, branching, depth), root length and growth, as well as root hairs and mycorrhiza-related traits play an important role in determining the capacity of plants to cope with the poor mobility of soil K, as well as its distribution in the whole soil profile, with potential significant contribution of subsoil K in many soils. Another consequence of the root-induced depletion of K^+ is a shift of the exchange equilibria, enhancing the desorption of exchangeable K, as well as the release of nonexchangeable, interlayer K from micaceous minerals in the rhizosphere. This means that both of these pools can be bioavailable, provided that plant roots can take up significant amounts of K at low K^+ concentrations in the soil solution (in the micromolar range). This is thus an important physiological root trait determining the acquisition efficiency of plants. Besides, roots can significantly acidify their environment or release large amounts of exudates, these two processes ultimately promoting the dissolution of K-bearing silicates such as micas and feldspars in the rhizosphere, which contributes the mining strategy evolved by plants. There are thus a number of root or rhizosphere-related traits (either morphological or physiological) that determine the acquisition efficiency of crop species and genotypes. The aim of this paper is to provide a detailed overview of these.

INTRODUCTION

Responding to global change represents a major challenge for the human race in the 21st Century, with the often competing demands of maintaining food security to feed a growing world population while reducing the impacts on the environment a case in point. While the Green Revolution achieved considerable increases in crop production and yield, almost matching the rate of population growth, it relied on the intensification of agriculture through the combination of improved crop genotypes, much increased use of fertilizers and pesticides, increased mechanization and irrigation (Tilman 1999). The widespread use of fertilizers has deeply modified the biogeochemical cycles of major nutrients (Vitousek et al. 1997), with impacts of nitrogen (N) and phosphorus (P) flows beyond the so-called planetary boundaries (Rockström et al. 2009). Losses from agricultural land are by far the largest contributors (Steffen et al. 2015), with excess use of N and P fertilizers in regions of intensive agriculture such as parts of the USA, Western Europe and China (Steffen et al. 2015). This has led to environmental damage through the emission of N_2O , which has a significant impact on global warming, and more locally to the pollution of groundwater bodies by nitrate and the eutrophication of surface waters in lakes and coastal sea waters. Potassium (K) fertilizers do not have such negative impacts when used in excess but, like P fertilizers, are derived from finite ores that are far from evenly distributed internationally (Manning et al. 2010). The increasing demand for N, P and K fertilizers and the energy cost of their fabrication and transportation result in rising prices and price fluctuations, with increased volatility expected in the coming decades (Brunelle et

al. 2015). This price volatility can have dramatic impacts in terms of food security, with a recent example occurring in 2008. A major challenge will be to use fertilizers in agriculture more efficiently worldwide, diminishing their use in regions where overuse is well documented, but increasing their use in situations where large nutrient deficits are being recorded. Many countries in Africa are in the latter situation (Manning et al. 2010). Further intensification of agroecosystems will require a paradigm shift, with sustainable development (i.e. aiming for ecological or sustainable intensification) as the primary target (Cassman et al. 1999; Tillman 1999). As noted by Lynch (2007) in his paper entitled “The Roots of the Second Green Revolution”, part of this paradigm shift resides in dedicating greater research and breeding efforts to identifying plant traits determining nutrient (and water) acquisition, by focusing on root and rhizosphere¹-related traits. This is the topic of this chapter. Lynch (2007) stressed that, while the Green Revolution selected crop genotypes responsive to high fertility (breeding for intense use of fertilizers and other inputs), the Second Green Revolution shall rather breed genotypes able to cope with low fertility, hence the need to place greater emphasis on belowground traits to achieve improved potassium acquisition efficiency (White 2013; White et al. 2013).

SOIL FEATURES DETERMINING THE FATE OF POTASSIUM AT THE SOIL-ROOT INTERFACE

A number of soil characteristics determine K mobility², availability and bioavailability (as defined below) to plants. These properties, together with the actual distribution of the various pools of K in the soil profile and horizons, ultimately determine the most desirable root and rhizosphere-related traits to search for to improve K acquisition efficiency in crops.

Potassium Mobility – Mass-Flow versus Diffusion in the Rhizosphere

Potassium is present as K⁺ in the soil solution, which experiences rather strong interactions (adsorption/desorption) with the many soil constituents contributing to cation exchange capacity, notably clay minerals and organic matter (Sparks and Huang 1985; Sparks 1987; Bell et al. 2017). The consequences of such interactions are two-fold. First, they buffer the concentration of K⁺ in the soil solution to values that commonly range from one to several hundred micromoles per dm³ (Asher and Ozanne 1967; Hinsinger 2006), which are significantly greater than those of phosphate but less than those of nitrate. Second, they limit K mobility in the soil. Thus, compared with nitrate, K leaching occurs in significant amounts only in fertilized, light-textured soils. In addition, while mass-flow can contribute significantly to the transport of nitrate towards the root surface as a consequence of transpiration-driven water uptake and corresponding solute movement, its contribution to the supply of K⁺ and phosphate ions is rather negligible (Barber 1995). Hence most K⁺ is transported to the root surface by diffusion, as a consequence of the concentration gradients that develop in the rhizosphere (Tinker and Nye 2001; Jungk 2002). Barber (1995) estimated in the Chalmers silt loam (mollisol) that diffusion contributed about 80% of the K delivered to maize roots.

Potassium Availability and Bioavailability – Exchangeable versus Nonexchangeable Pools in the Rhizosphere

The environmental availability of a nutrient is an intrinsic property of the soil that is usually assessed by chemical methods designed to extract that fraction of the nutrient that is likely to replenish the soil solution in response to depletion by nutrient uptake (Harmsen et al. 2005; Harmsen 2007). It is usually expressed as a concentration, while the environmental bioavailability is best defined as the actual flux of a nutrient into a living organism (Harmsen et al. 2005; Harmsen 2007), which means that it varies for a

¹ Rhizosphere is here defined as the volume of soil around living roots that is influenced by root activities (e.g. Hinsinger et al. 2009)

² The mobility is meant here to describe the ability of K⁺-ions to be transferred in soils, either vertically through leaching or laterally, through mass-flow and diffusion (e.g. Hinsinger 2004).

given soil, nutrient and set of environmental conditions, as well as the organism of interest (e.g. the plant species or genotype). This is due to both differences in uptake capacities and abilities to alter the availability in the bio-influenced zone (Harmsen et al. 2005), which corresponds to the rhizosphere for plants (Hinsinger et al. 2011). For K, it was long assumed that the only available pools were K^+ in the soil solution and adsorbed onto negatively-charged soil constituents (Sparks and Huang 1985; Sparks 1987), which is often assessed via an extraction with ammonium salts. These correspond to the so-called exchangeable K pool that represents typically about 1-2% of total soil K (Bell et al. 2017). It has been well documented that plants can exploit this pool, which is therefore bioavailable. Most of soil K is, however, non-exchangeable in the sense that it cannot be extracted by an ammonium salt. There are two main non-exchangeable pools, corresponding to either K^+ contained in the interlayer of micaceous minerals (primary minerals such as micas and secondary minerals such as illites and illite-like clay minerals) or in the structure of other K-bearing silicates, feldspars being the most abundant ones (Sparks and Huang 1985; Sparks 1987). These are called interlayer K and structural K, respectively, and used to be considered as poorly available or non-available. However, there has been growing evidence that they are bioavailable to some plants, as further explained below (Hinsinger 2006; Hinsinger 2013).

Potassium Distribution – Topsoil versus Subsoil K Availability

It is often assumed that the topsoil is enriched in nutrients compared to the subsoil, or at least exhibits greater nutrient availability. This occurs in many natural ecosystems due to the role of vegetation in the rapid recycling of nutrients through uptake and litterfall as well as throughfall, the latter being especially important for K. Nutrients therefore accumulate in the topsoil, and whenever uptake occurs at greater depth, this ultimately contributes to nutrient uplift (Jobbagy and Jackson 2001). In agroecosystems, the topsoil can be enriched by K fertilization but there is also some evidence for K uplift (Barré et al. 2009), which points to a significant uptake of K occurring in the subsoil. This overlooked component of the soil, namely the subsoil and the potential reservoir of available nutrients it can represent, has been recently reviewed by Kautz et al. (2013), who stressed the need to assess its contribution to plant nutrition further. Kuhlmann (1990) provided some quantitative assessment of the contribution of the subsoil to wheat K nutrition, which ranged from 7 to 70%, with an average of 34% in luvisols of Northern Germany. The contribution may be less in deeply weathered soils such as oxisols and ultisols, which contain less exchangeable and nonexchangeable stocks. However, for deep-rooted plants such as eucalypt in deep oxisols in Brazil, we have recently shown that significant root-soil interactions occur at considerable depths, affecting the fate of K to at least 4 m (Pradier et al. 2017). This reinforces the need to take subsoil K into consideration in future research and in K-fertilizer prescriptions, as well as when designing more K-efficient ideotypes of crops in breeding programs.

ROOT MORPHOLOGICAL TRAITS DETERMINING THE ACQUISITION OF POTASSIUM BY PLANTS

Because of the restricted mobility of various nutrient ions, including K^+ , NH_4^+ and phosphate in soils, plants have evolved a range of strategies to forage for them by increasing of the volume of their rhizosphere, i.e. the actual volume of soil from which they can acquire these poorly mobile nutrients (Hinsinger 2004; Lynch 2007; Hinsinger et al. 2011).

Root System Architecture and Plasticity

Plant species can differ considerably in root system architecture (RSA) with the tap-rooted systems and fibrous systems found in crops good examples (Kutschera et al. 2009). Tap-rooted systems usually enable plants to access deeper horizons, while colonizing the topsoil less densely than fibrous systems. Witter and Johansson (2001) compared forage species and estimated that the tap- and deep-rooted alfalfa obtained about 67% of its K from the subsoil, while ryegrass, with its fibrous root system, obtained only 42% of its K from the subsoil under the same conditions. While the type of RSA (e.g. tap-rooted vs fibrous) is genetically determined, it has been shown that there is considerable variation in RSA within a given species, which is a promising avenue for selecting more efficient crop genotypes of a broad range

of species (Lynch 2007 and 2015; Hammond et al. 2009; White et al. 2013; Mi et al. 2016; Thomas et al. 2016). While most of the work done so far has been conducted for N or P, some of these results can be easily extended to K. The root angle and distance between lateral roots are traits that will largely determine inter-root competition and the overlapping of the rhizosphere of neighboring roots, which is of greater importance for mobile resources, such as water and nitrate, than for poorly mobile nutrients such as K or P (Ge et al. 2000). Lynch and co-workers have shown in common bean and maize that shallow-rooted genotypes may perform better than deep-rooted genotypes whenever there is a strong vertical gradient of fertility, with much greater nutrient availability in the topsoil than in the subsoil (Ge et al. 2000), and that past breeding schemes have resulted in selecting more shallow root systems in maize in the USA (York et al. 2015). Their work has also shown considerable plasticity of RSA traits that can vary substantially with sowing density for instance. Such plasticity is an intrinsic property of root systems, which further complicate their study and phenotyping, but which plays a major role in the adaptive strategy of plants. In contrast to N and P, plants do not seem to respond to K-rich patches by enhanced root proliferation (Drew 1975; Hermans et al. 2006), which may restrict the options for effective fertilizer K placement, unless co-located with N or P. Nevertheless, although breeders are still reluctant, there is considerable progress to be expected from integrating RSA-related traits into breeding programs, and this is urgently needed to obtain genotypes that can cope better with spatially restricted availability of nutrients such as N, P or K (Lynch 2015).

Root Length and Growth

For poorly mobile nutrients it has long been known that root length or root area are amongst the most relevant traits determining their acquisition (Barber 1995). In their sensitivity analysis, Silberbush and Barber (1983) showed that the predicted K acquisition by soybean was increased more by an increase in root area than by the same relative increase in any other parameter in their classic Barber-Cushman model. More recently, Wissuwa (2003) predicted that a 22% increase in the root surface area of rice was enough to give a 3-fold increase in P acquisition under P-limiting conditions. Given that the mobility of K^+ is greater than that of phosphate in soils, it is likely that an even smaller change of root surface area would have a significant impact on K acquisition. In this respect, the modelling work by Pagès (2011), conducted with a more realistic distribution of roots based on RSA, rather than an evenly distributed root system as in the Barber-Cushman models, revealed that greater root length was ecologically relevant for the acquisition of poorly mobile nutrients, such as P, but not for mobile ions, such as nitrate (due to large overlapping of nitrate depletion zones). The results for K^+ and ammonium ions were intermediate.

Genotypes within a species can exhibit considerable variation in root length as shown for example for potato (Wishart et al. 2013) or maize (Erel et al. 2017). While the relationship between crop performance (growth or yield) under nutrient-limiting conditions and root length was not consistently significant or positive, these studies suggest exploring the impact of root length variation is worthy of more detailed investigation. While root length was weakly correlated with K uptake in a range of lentil genotypes, Gahoonia et al. (2006) showed that root hair length was an even more relevant root trait for poorly mobile nutrients such as K or P. As for RSA, root length and related traits such as specific root length or root surface area are not just genetically determined but are also highly plastic, responding to many environmental factors and biological stimuli. Plant growth promoting microorganisms are an example of the latter, with some of these directly altering root growth or proliferation (Vacheron et al. 2013).

Root Hairs and Mycorrhiza

It has been well documented for the least mobile nutrients, such as P, that morphological/anatomical features other than RSA and root length related traits can play a major role in extending the rhizosphere volume, and hence the actual amount of nutrient acquired. These include root hairs that can extend up to several mm from the root surface (e.g. Gahoonia et al. 1997), and mycorrhizal hyphae, which can access even greater volumes, extending up to several cm from the root surface (e.g. Jakobsen et al. 1992; Thonar et al. 2011). Their direct implication for the acquisition of K^+ is less well documented, but there are a

number of reports on the potential role of root hairs and mycorrhiza-related traits for improving the foraging capacity of plants for soil K. In their modelling of K uptake Samal et al. (2012) showed that, assuming root hair surface areas ranging from 0.38 to 0.47 cm² cm⁻² root, root hairs contributed slightly less to K uptake than the roots alone (without their root hairs) in wheat and maize, but more than the roots alone in sugarbeet. The significant role of root hairs in K acquisition is also supported by the good correlation between root hair length and K acquisition found among crop species in decreasing order of efficiency: oilseed rape, tomato, ryegrass, maize, onion (Claassen and Jungk 1984; Jungk 2001) or rye, ryegrass, oilseed rape, alfalfa, barley, pea, red clover (Høgh-Jensen and Pedersen 2003). Høgh-Jensen and Pedersen (2003) also reported some plasticity for this trait as root hairs exhibited greater length at lower K supply, suggesting a relevant, adaptive strategy for improving K acquisition. Mycorrhizal hyphae can access a much greater volume of soil than roots and, thereby, increase the effective radius of the rhizosphere. While their quantitative impact on K acquisition has been studied much less than for P acquisition, the K uptake transport systems involved in the mycorrhizal symbiosis are now well documented (Garcia and Zimmermann 2014). Additional research is needed on the functional side of this symbiosis before identifying relevant traits worthy of being pursued for improving K acquisition efficiency.

ROOT PHYSIOLOGICAL TRAITS DETERMINING THE ACQUISITION OF POTASSIUM BY PLANTS

As potassium is present only as K⁺ in soils, which interacts strongly with negatively charged soil constituents or is part of the crystal lattice of silicate minerals, K acquisition by plants is dependent on the mobilization of K from these sources. Depletion of K⁺ in the rhizosphere solution and the excretion of protons and other K-mobilizing exudates (a 'mining' strategy) can increase the availability of K for plant nutrition (Hinsinger et al. 2011).

Traits Related to Potassium Uptake and Depletion in the Rhizosphere

For poorly mobile nutrients, such as P or K, the uptake capacity of root cells, determined by the rate of transport of ions across the plasma membrane, is not the limiting step for their acquisition. This contrasts markedly with the situation for more mobile nutrients, such as nitrate, as confirmed by sensitivity analysis of Barber-Cushman and other models (Rengel 1993). Nevertheless, in the case of K, the uptake of K⁺ is a driving process for accessing both the exchangeable pool and even a significant part of the nonexchangeable pool (Hinsinger 2006, Hinsinger et al. 2011; White et al. 2013). When roots take up K⁺ from the soil solution, there is a rapid depletion of K⁺ in the rhizosphere. This was first observed in the early 1960s using autoradiography of a radioactive analogue of K, ⁸⁶Rb, which demonstrated the occurrence of a depletion zone extending a few mm from the surface of maize roots (Walker and Barber 1962), and was later confirmed by a range of approaches, based on direct measurements or modelling (e.g. Kuchenbuch and Jungk 1982; Claassen et al. 1986). The latter studies also demonstrate that K⁺ uptake by roots can deplete the exchangeable pool of K by causing a shift in the cation exchange equilibria towards enhanced desorption of K⁺ ions. As plant roots are capable of decreasing the concentration of K⁺ from several hundreds of micromoles per dm⁻³ in the bulk soil down to concentrations in the micromolar range at the root surface, they can even shift the equilibria determining the release of interlayer K in micaceous phyllosilicate minerals (illites, illite-like clay minerals and micas), ultimately depleting the large pool of nonexchangeable K contained in soils (Kuchenbuch and Jungk 1982; Niebes et al. 1993; Moritsuka et al. 2004) and altering soil mineralogy (Kodama et al. 1992; Barré et al. 2007 and 2008). We demonstrated the occurrence of this mechanism in the rhizosphere of ryegrass by using a phlogopite mica as sole source of (almost exclusively interlayer) K, which released significant amounts of interlayer K and caused the concomitant transformation of the mica into a vermiculite clay mineral within only a few days of growth (Hinsinger et al. 1992; Hinsinger and Jaillard 1993). Barré et al. (2007) further confirmed this alteration of soil mineralogy for illitic clay minerals in the rhizosphere of ryegrass in a pot experiment, and this was also shown recently in a field experiment with maize (Adamo et al. 2016). Springob and Richter (1998) have shown that the rate of release of nonexchangeable K in soils can be

considerably enhanced below a threshold K^+ concentration of about 2-3 micromoles per dm^{-3} , which is the order of concentrations occurring close to root surface as a consequence of K^+ uptake and subsequent depletion of K in the rhizosphere (Claassen and Jungk 1982; Hinsinger 2006). In this respect, two important uptake characteristics to account for are the C_{min} value (minimal concentration below which plant cannot take up K) and the capacity to achieve a large K uptake rate at low K^+ ion concentrations, which depends on the K_m parameter of the Michaelis-Menten equation. In other words, plant species or genotypes showing very low C_{min} values (Asher and Ozanne 1967) and high affinity (low K_m) of their K transporters, would be better equipped for depleting K^+ ions to concentrations low enough to induce a significant release of interlayer K and thus access the large pool of nonexchangeable K that would be otherwise unavailable. Such K uptake traits differ between and within plant species and might be worth considering for screening K-efficient crop genotypes (White 2013; White et al. 2016).

Traits Related to pH Modification in the Rhizosphere

It should be noted that a number of field experiments have reported an increase of some K pools, notably the exchangeable K pool, in the rhizosphere instead of a depletion. This has been shown mostly in perennial tree species, e.g. by Courchesne and Gobran (1997) in a Norway spruce forest, Bourbia et al. (2013) in an olive grove and Pradier et al. (2017) in a eucalypt plantation. These observations strongly suggest the occurrence of root-induced weathering processes, resulting in an increase of exchangeable K at the expense of the nonexchangeable K pool through other processes than those mentioned above. For instance, Pradier et al. (2017) showed that root-induced acidification of the rhizosphere of eucalypt trees may have partly contributed to the increase of exchangeable K that was observed throughout the soil profile down to a depth of 4 m. Plant roots can modify rhizosphere pH considerably and root-mediated acidification of up to 2-3 pH units has been observed repeatedly (e.g. Römheld 1986; Hinsinger et al. 2003; Blossfeld et al. 2013). Such a decrease of pH can have a dramatic effect on the weathering rate of minerals such as K-bearing silicates, through proton-promoted dissolution (Berner et al. 2003; Taylor et al. 2009; Hinsinger 2013).

The ability to modify rhizosphere pH varies between plant species. For instance, faba bean reduces rhizosphere pH more effectively than maize (Liu et al. 2016) and oilseed rape induces a dissolution of the phlogopite mica as a consequence of rhizosphere acidification, while ryegrass does not (Hinsinger et al. 1993). The latter phenomenon has not been widely studied in crops to our knowledge, but a number of studies have been conducted in the context of forest trees. For example, Arocena et al. (1999) showed that the acidification occurring around ectomycorrhizas could have been involved in the dissolution of micas and feldspars. The capacity of roots to change the rhizosphere pH is not a simple trait to target, as root-mediated pH changes are essentially the consequence of an imbalanced uptake of major cations and anions (Hinsinger et al. 2003). Rhizosphere acidification occurs when a net surplus of major cations (K^+ being often predominant in the cation budget of plants) are taken up relative to the sum of major anions. Thus, there are many ways to increase rhizosphere acidification but it is not expected to be related to a single trait, as the underlying mechanisms are largely determined by the environmental context. Nevertheless, plant species or genotypes could be screened quite easily for their capacity to acidify their rhizosphere in a given context (Gahoonia et al. 2006).

Traits Related to Exudation in the Rhizosphere

Besides protons, roots can release large quantities of diverse exudates, including some that can also promote the dissolution of K-bearing silicates. Examples of these include carboxylates such as citrate, oxalate and malate, which are able to complex cations contained in the crystal lattice of these minerals (Jones 1998). These exudates can thus be involved in the ligand-promoted dissolution of feldspars and micas (Razzhage and Robert 1979; Robert and Berthelin 1986; Song and Huang 1988; Barman et al. 1992; Lawrence et al. 2014), and thus enhance the release of nonexchangeable K, i.e. structural and interlayer K, respectively, together with the other metal cations contained in these silicates. Screening wheat and maize and sorghum genotypes for their release of malate and citrate, respectively, to detoxify

Al has been successful, which shows that such a trait can vary substantially within some plant species (e.g. Ryan et al. 2011). However variations are certainly greater between species, with some crops such as white lupin or chickpea being renowned for their large carboxylate exudation capacity (Jones 1998). Even minute amounts of malate or citrate exuded at the root tip may provide sufficient protection against Al toxicity (Ryan et al. 2011), but much high concentrations would be needed to induce significant release of K through ligand-promoted dissolution of K-bearing silicates. There is no direct evidence to our knowledge that such exudation traits are worth pursuing for improving K acquisition efficiency in crops. Exudation is nonetheless a complex and major process occurring in the rhizosphere, which stimulates the microbial communities and has potential implications in the dissolution of nutrient-bearing minerals (e.g. Philippot et al. 2013), as reviewed for fungi by Hoffland et al. (2004).

CONCLUSION

A number of root or rhizosphere-related traits determine the K acquisition efficiency of crops, influencing both their foraging and mining for K^+ . To deal with the restricted mobility of K^+ ions in soils, the foraging strategy of plants is based on a number of root traits: densely branched root system architectures with substantial portions exploring the topsoil and the subsoil, with a large root surface area or length are desirable traits. In addition, roots can extend the volume of exploited soil and the K depletion zones considerably by developing long root hairs or supporting strong mycorrhizal symbioses. In addition to this foraging strategy, which extends the size of the rhizosphere, plants have also evolved various mining strategies to increase the availability of the so-called poorly-available pools of K in the rhizosphere. The corresponding traits are related first to the ability of roots to sustain high fluxes of K at very low concentrations in the soil solution. This induces a shift in the exchange equilibria and an enhanced desorption of exchangeable K, as well as an enhanced release of nonexchangeable, interlayer K contained in micaceous minerals. Second, roots can promote the dissolution of K-bearing silicates such as micas and feldspars through rhizosphere acidification and/or exudation of complexing ligands such as some carboxylates. How to make better use of these traits in the context of a sustainable intensification of agroecosystems is not so obvious though, and breeders have not been integrating belowground traits in their breeding schemes. To do so may introduce additional challenges, such as potential trade-offs with those traits required for the acquisition of other resources (water, N, P, micronutrients).

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