Potassium Use Efficiency of Plants

Philip J White, Michael J Bell, Ivica Djalovic, Philippe Hinsinger, Zed Rengel

Chapter 5
Potassium Use Efficiency of Plants

Philip J. White, Michael J. Bell, Ivica Djalovic, Philippe Hinsinger, and Zed Rengel

Abstract There are many terms used to define aspects of potassium (K) use efficiency of plants. The terms used most frequently in an agricultural context are (1) agronomic K use efficiency (KUE), which is defined as yield per unit K available to a crop and is numerically equal to the product of (2) the K uptake efficiency (KUpE) of the crop, which is defined as crop K content per unit K available and (3) its K utilization efficiency (KUtE), which is defined as yield per unit crop K content. There is considerable genetic variation between and within plant species in KUE, KUpE, and KUtE. Root systems of genotypes with greatest KUpE often have an ability (1) to exploit the soil volume effectively, (2) to manipulate the rhizosphere to release nonexchangeable K from soil, and (3) to take up K at low rhizosphere K concentrations. Genotypes with greatest KUtE have the ability (1) to redistribute K from older to younger tissues to maintain growth and photosynthesis and (2) to reduce vacuolar K concentration, while maintaining an appropriate K concentration in metabolically active subcellular compartments, either by anatomical adaptation or

P. J. White (✉)
Ecological Sciences, The James Hutton Institute, Dundee, UK

King Saud University, Riyadh, Saudi Arabia
e-mail: philip.white@hutton.ac.uk

M. J. Bell
School of Agriculture and Food Sciences, The University of Queensland, Brisbane, QLD, Australia
e-mail: m.bell4@uq.edu.au

I. Djalovic
Institute of Field and Vegetable Crops, Novi Sad, Serbia
e-mail: ivica.djalovic@ifvcns.ns.ac.rs

P. Hinsinger
Eco&Sols, University of Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France
e-mail: philippe.hinsinger@inrae.fr

Z. Rengel
Soil Science and Plant Nutrition M087, School of Agriculture and Environmental Science, University of Western Australia, Crawley, WA, Australia
e-mail: zed.rengel@uwa.edu.au

T. S. Murrell et al. (eds.), *Improving Potassium Recommendations for Agricultural Crops*, https://doi.org/10.1007/978-3-030-59197-7_5

by greater substitution of K with other solutes in the vacuole. Genetic variation in traits related to KUpE and KUtE might be exploited in breeding crop genotypes that require less K fertilizer. This could reduce fertilizer costs, protect the environment, and slow the exhaustion of nonrenewable resources.

5.1 Metrics of Potassium Use Efficiency and Their Relationships

There are many terms defining aspects of the potassium (K) use efficiency of plants (Table 5.1; White 2013). The terms used most frequently in an agricultural context are (1) agronomic K use efficiency (KUE), which is defined as crop yield (Y) per unit K available (Ka) from the soil plus fertilizer (g Y g^{-1} Ka) and is numerically equal to the product of (2) the K uptake efficiency (KUpE) of a crop, which is defined as crop K content (K_{crop}) per unit K available in the soil plus fertilizer (g K_{crop} g^{-1} Ka) and (3) its K utilization efficiency (KUtE), which is defined as yield per unit crop K content (g Y g^{-1} K_{crop}). These are often complemented by measurements of (4) the

Table 5.1 Mathematical definitions of aspects of potassium (K) use efficiency in crops

	Name	Abbreviation	Calculation	Units
1	Agronomic K use efficiency	KUE	Y/Ka	g DM g^{-1} K
2	K uptake efficiency	KUpE	K_{crop}/Ka	g K g^{-1} K
3	K utilization efficiency	KUtE	Y/K_{crop}	g DM g^{-1} K
4	Yield response to K supply		$Y = Y_{max} \times (Ka/(Km_{Ka} + Ka))$	
5	Response of plant K content to K supply		Derived from Eqs. (4) and (6)	
6	Yield response to plant K content		$Y = Y_{max} \times (K_{crop}/(Km_{Kcrop} + K_{crop}))$	
7	Apparent fertilizer recovery efficiency	ARE	$((K_{crop(Kf)} - K_{crop(Ks)})/Kf) \times 100$	%
8	Agronomic efficiency of K fertilizer	AE	$(Y_{Kf} - Y_{Ks})/Kf$	g DM g^{-1} K
9	Root uptake capacity		K_{crop}/R	g K g^{-1} DM
10	Apparent remobilization efficiency	AKR	$((K_{tissue(o)} - K_{tissue(t)})/K_{tissue(0)}) \times 100$	%

Abbreviations: DM = dry matter, Ka = K available from both soil and fertilizer, K_{crop} = crop K content, $K_{crop(Kf)}$ = crop K content when fertilizer is applied, $K_{crop(Ks)}$ = crop K content without fertilizer, $K_{crop(max)}$ = maximum crop K content, $K_{tissue(o)}$ = original tissue K content, $K_{tissue(t)}$ = tissue K content after remobilization, Km_{Ka} = Ka at which Y equals $Y_{max}/2$, Km_{Kcrop} = K_{crop} at which Y equals $Y_{max}/2$, Kf = K supplied as fertilizer, Ks = available K in soil with no fertilizer applied, R = root DM, Y = yield, Y_{Kf} = yield with fertilizer applied, Y_{Ks} = yield without fertilizer applied, Y_{max} = maximum yield

For further information see Fageria (2009), White (2013), Maillard et al. (2015) and White et al. (2016)

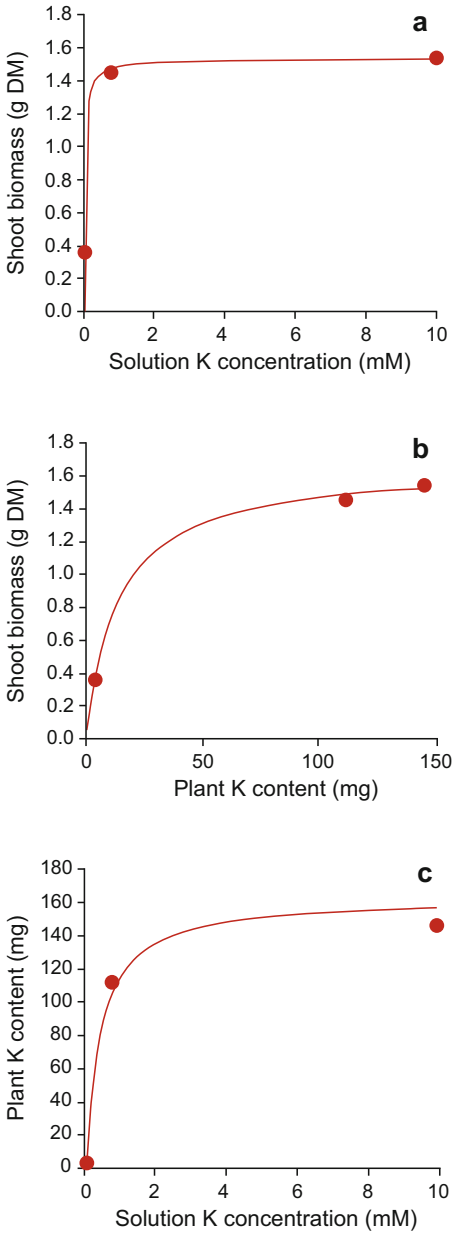

Fig. 5.1 Relationships between (**a**) shoot dry biomass and the K concentration in the nutrient solution, (**b**) shoot dry biomass and plant K content, and (**c**) plant K content and the K concentration in the nutrient solution for seedlings of spring barley "Prisma" grown hydroponically for 21 days in complete nutrient solutions containing 10 μM, 0.75 mM, or 10 mM K^+. Lines show regressions to the data assuming Michaelis–Menten relationships with (**a**) $Km_{Ka} = 0.032$ mM and $Y_{max} = 1.53$ g DM, (**b**) $Km_{Kcrop} = 13.9$ mg K and $Y_{max} = 1.66$ g DM, and (**c**) the relationship between shoot K content and the K concentration in the nutrient solution predicted using these regressions. (data from White et al. 2016)

response of crop yield to K availability, (5) the response of crop K content, or tissue K concentration, to K availability, and (6) the relationship between crop yield and crop K content or tissue K concentration (Figs. 5.1 and 5.2). In practice, these

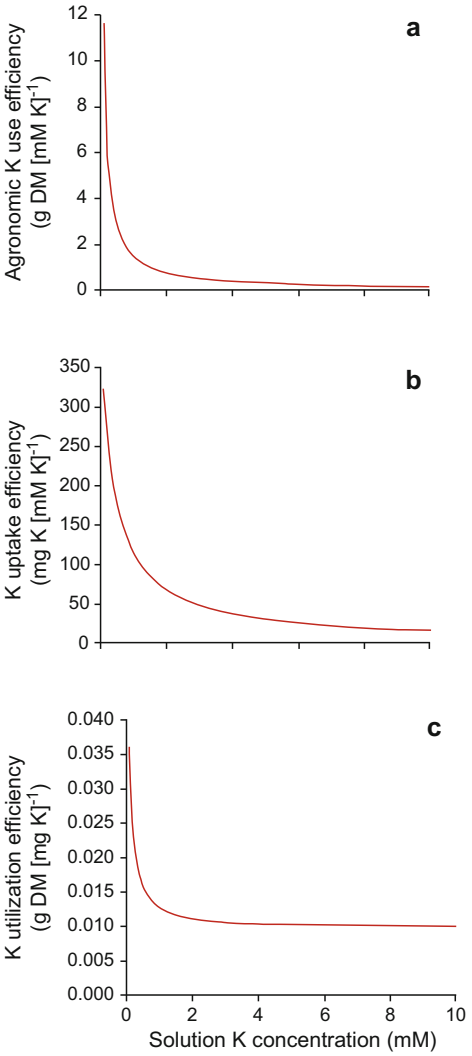

Fig. 5.2 Relationships between (**a**) agronomic K use efficiency (KUE) and the K concentration in the nutrient solution, (**b**) K uptake efficiency (KUpE) and the K concentration in the nutrient solution, and (**c**) K utilization efficiency (KUtE) and the K concentration in the nutrient solution for seedlings of spring barley "Prisma" grown hydroponically for 21 days in complete nutrient solutions containing various K concentrations. Lines were calculated from the data shown in Fig. 5.1. (White et al. 2016)

relationships are difficult to determine accurately even when data are obtained at many K availabilities and depend upon many environmental factors.

Other frequent assessments include (7) the apparent recovery (acquisition) of applied K fertilizer, which is numerically equal to KUpE when there is no available K in the unfertilized soil but is proportionally decreased as the available K in the unfertilized soil increases, and (8) the increased crop yield resulting from the application of K fertilizers relative to the amount of K fertilizer applied (Fageria 2009). The latter is often referred to as K fertilizer use efficiency or agronomic efficiency (AE). It can be determined relatively simply in field experiments, but the values obtained depend upon a variety of environmental factors, including the K

availability in the unfertilized soil and factors affecting K acquisition, plant growth rates, and harvest index. The ability of a plant to tolerate low K availability can be expressed as the proportion of yield potential that it achieves without the application of K fertilizer (Rengel and Damon 2008). There are differences in all these aspects of K use efficiency both between and within plant species. This chapter describes plant traits affecting these characteristics and highlights those that commonly account for differences in KUE, KUpE, and KUtE between and within plant species.

5.2 Differences in Potassium Uptake and Utilization Between Plant Species

Plant species differ in their growth response to K supply either because of differences in their ability to acquire K from the soil (KUpE) or their ability to utilize K physiologically (KUtE) for vegetative and reproductive growth (Fageria 2009; Römheld and Kirkby 2010; White 2013; White and Bell 2017). Plant roots can acquire sufficient K for maximal growth from solutions containing micromolar K concentrations, provided the K supply to the roots matches the minimal K demand of the plant and the concentration of ammonium, which competes with K^+ for transport and inhibits the expression of genes encoding the dominant high-affinity H^+-coupled K^+ transporter in roots (e.g., *AtHAK5* in arabidopsis, *Arabidopsis thaliana* (L.) Heynh.; Qi et al. 2008), in the rhizosphere is small (Asher and Ozanne 1967; Wild et al. 1974; Spear et al. 1978a; Siddiqi and Glass 1983a; White 1993). The minimum tissue K concentration that can be tolerated without impacting plant growth and development must be sufficient to maintain about 100 mM K^+ in metabolically active compartments including the cytosol, mitochondria, and plastids (White and Karley 2010). This requires a minimal vacuolar K^+ concentration in living cells of 10–20 mM, which corresponds to a tissue K concentration of 5–40 mg g^{-1} dry weight (White and Karley 2010; White 2013).

Species from the Poales and Brassicales generally achieve their growth potential at a lower K supply than many other angiosperms and compete best in K-limited environments (Asher and Ozanne 1967; Hoveland et al. 1976; Grant et al. 2007; Hafsi et al. 2011; White et al. 2012). Species from these orders are, therefore, considered to be tolerant to K deficiency (i.e., K-efficient; Rengel and Damon 2008). Similarly, cereal and brassica crops generally require less K fertilizer than most vegetable, solanaceous, or beet (*Beta vulgaris* L.) crops to achieve maximum yields (Greenwood et al. 1980; Pretty and Stangel 1985; Steingrobe and Claassen 2000; Brennan and Bolland 2004; Trehan 2005; Fageria 2009; Kuchenbuch and Buczko 2011; Brennan and Bell 2013; Trehan and Singh 2013; White 2013; Schilling et al. 2016). Other crops that have a large demand for K fertilizer include oil palm (*Elaeis guineensis* Jacq.) and banana (*Musa acuminata* Colla/*Musa balbisiana* Colla) grown in plantations (Mengel et al. 2001; White 2020).

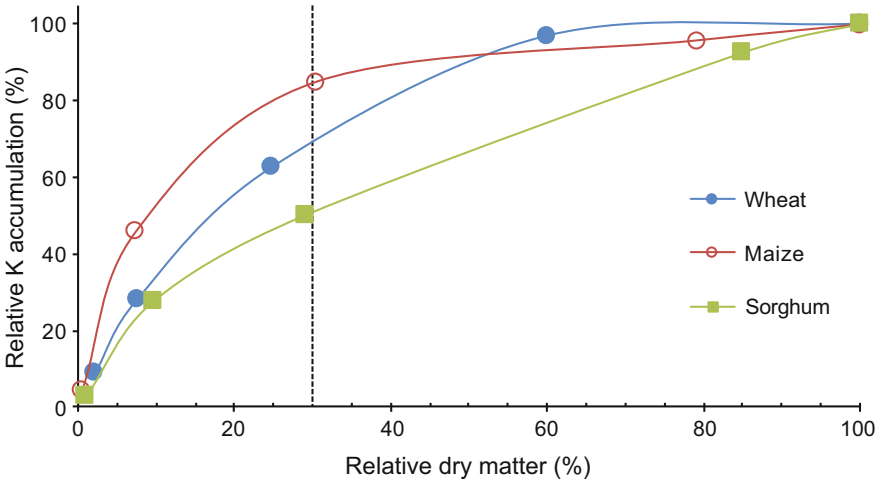

Fig. 5.3 Relative accumulation of dry matter and potassium (K) in wheat, maize, and sorghum grown to maturity in an Oxisol soil under controlled conditions in the glasshouse (Bell et al. unpublished). Maize shows the classic K accumulation curve that is well in advance of biomass in relative terms, with >80% of total K uptake occurring in the first third of the growing season (when relative biomass accumulation is only ~30%). Wheat shows a similar tendency, although relative K accumulation occurs less rapidly than in maize, while grain sorghum shows accumulation that more closely reflects the pattern of dry matter accumulation

Crops also differ in their temporal demand for K, which is related to their individual phenology, and K supply must be synchronized with their K demand to achieve maximal yields (White 2013). For example, both maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) accumulate K during early growth, while grain sorghum (*Sorghum bicolor* [L.] Moench) accumulates K roughly in proportion to its biomass accumulation (Fig. 5.3). One explanation for the temporal difference in K accumulation between these species might be tillering: The main stems of wheat and sorghum show an almost identical pattern of relative accumulation of K and DM as the uniculm maize, but the subsequent production of tillers requires continued K accumulation in new vegetative structures. While tillering in wheat occurs at a similar time to the development of the main stem, tillering in sorghum continues until much later in crop development.

5.2.1 Differences in KUpE Between Plant Species

Differences between plant species in their ability to acquire K from the soil has been attributed to differences in (1) the capacity of their root cells to take up K^+ at low rhizosphere K^+ concentrations, (2) the ability of their root systems to proliferate and exploit the soil volume effectively, and (3) their ability to acquire nonexchangeable K from the soil (Greenwood et al. 1980; Steingrobe and Claassen 2000; Wang et al.

2000, 2011; Jungk 2001; Rengel and Damon 2008; El Dessougi et al. 2010; Römheld and Kirkby 2010; Samal et al. 2010; White 2013; White et al. 2017).

5.2.1.1 Kinetics of Potassium Uptake

The uptake of K and its movement within plants are dynamic processes involving many transport proteins in many cellular membranes (White and Karley 2010; White and Bell 2017). These transporters are regulated precisely to ensure K homeostasis in metabolic compartments (White and Karley 2010; Véry et al. 2014; Nieves-Cordones et al. 2016). Thus, the relationship between K uptake by plant roots and the K concentration in the rhizosphere solution can vary markedly, both spatially and temporally, as the plant matches K supply and K demand through its K transport systems. When plants lack sufficient K, either because of low substrate K supply or high plant K demand for growth, there is an induction of genes encoding high-affinity K^+ transporters (Hermans et al. 2006; White and Karley 2010; Véry et al. 2014; Nieves-Cordones et al. 2016; White and Bell 2017), which not only increases cellular capacity for K uptake, but also increases the affinity for K in the rhizosphere solution. This reduces the K^+ concentration in the rhizosphere solution at K flux equilibrium. Indeed, the K^+ concentration at the root surface can decline to $<$2–3 μM, which not only accelerates K^+ diffusion to the root surface but also promotes the release of nonexchangeable K from soil minerals (Hinsinger 1998, 2013; Chap. 4).

When assayed under the same conditions, there are large differences between plant species in the maximal rate of K uptake, the solution K concentration at which K uptake is half maximal, and the minimal K concentration in the rhizosphere solution when there is K flux equilibrium. Plant species differ in both (1) the relationship between K uptake and the K concentration in the rhizosphere solution (e.g., Asher and Ozanne 1967; Wild et al. 1974; Spear et al. 1978a; Steingrobe and Claassen 2000; El Dessougi et al. 2002, 2010; Brennan and Bolland 2004; Wang et al. 2011; White 2013) and (2) the selectivity of monovalent cation accumulation (Broadley et al. 2004; Watanabe et al. 2007; White et al. 2012, 2017). This has been attributed to differences in both the capacity and complement of transport proteins catalyzing K^+ influx to root cells of different plant species (White 2013; Nieves-Cordones et al. 2016), although the molecular mechanisms, and evolutionary processes, underlying these differences are largely unknown. Roots of rapidly growing plant species with large shoot/root biomass quotients and a great K demand often have greater K uptake capacities than those of other plant species, and the roots of cereals and grasses generally have large K uptake capacities (Pettersson and Jensén 1983; Jungk and Claassen 1997; Steingrobe and Claassen 2000; Végh et al. 2008; Samal et al. 2010; Wang et al. 2011; Coskun et al. 2013). The ability of perennial ryegrass (*Lolium perenne* L.) to accumulate more K than grain amaranth (*Amaranthus* sp.) when, for example, phlogopite (1.6-fold difference) or vermiculite (12.8-fold difference) was the growth substrate was attributed to a greater K uptake

capacity and a lower K concentration at which there was net K uptake in perennial ryegrass than in grain amaranth (Wang et al. 2011).

5.2.1.2 Root System Investment and Architecture

A larger root system generally allows greater access to soil K and increasing the density of roots in soil can help reduce the K concentration in the rhizosphere solution, which accelerates K diffusion to the root and promotes the release of nonexchangeable K (Zörb et al. 2014). In general, grasses and cereals invest more in root biomass than other plants, which often results in rapid and effective exploitation of the soil volume, greater root density throughout the soil volume, and potentially deeper rooting (Steingrobe and Claassen 2000; Høgh-Jensen and Pedersen 2003; Végh et al. 2008; Samal et al. 2010; White 2013; Thorup-Kristensen et al. 2020). This effect is enhanced by increasing the specific surface area ($m^2\ g^{-1}$ DM) of roots, for example by producing a finer, more densely branched root system, which increases the contact between roots and soil for a given biomass investment (White et al. 2013). Thus, it has been hypothesized that plants with greater KUpE might have a relatively larger proportion of thin roots in their root system than those with lower KUpE (Rengel and Marschner 2005; Végh et al. 2008). In addition to differences in the absolute biomass investment in the root system, the placement of roots in the soil profile also differs between plant species (Gregory 2006; Hinsinger 2013; Thorup-Kristensen et al. 2020). Kuhlmann (1990) showed that plant species with deeper roots were more reliant on K located in the subsoil than those with shallower roots, which could sometimes make a major contribution to K uptake. When growing on sandy soils that are susceptible to K leaching, it can benefit plants to have deeper root systems to acquire K at depth (Ehdaie et al. 2010; Maeght et al. 2013).

An abundance of long root hairs also facilitates K uptake by roots. It increases both the volume of soil that is explored and the surface area of the root in contact with the soil. This enhances K depletion in the rhizosphere solution and creates a steeper K^+ diffusion gradient within the bulk soil solution (Rengel and Marschner 2005). This trait also differs between plant species (White 2013). Jungk (2001) reported a linear relationship between the specific rate of K uptake (mg K cm^{-1} root) and the length of root hairs among onion (*Allium cepa* L.), maize, perennial ryegrass, tomato (*Solanum lycopersicum* L.), and canola (oilseed rape; *Brassica napus* L.). Høgh-Jensen and Pedersen (2003) reported a linear relationship between K accumulation and root hair length among red clover (*Trifolium pratense* L.), pea (*Pisum sativum* L.), barley (*Hordeum vulgare* L.), alfalfa (*Medicago sativa* L.), canola, perennial ryegrass, and rye (*Secale cereale* L.), illustrating the importance of this trait for K uptake.

5.2.1.3 Rhizosphere Acidification and Root Exudates

Root-induced acidification of the rhizosphere can lead to a significant release of exchangeable K in soils (Hinsinger 2013; Hinsinger et al. 2017). Plant species differ in their ability to acidify the rhizosphere and access nonexchangeable K in the soil. For example, legumes reduce rhizosphere pH more effectively than cereals (Liu et al. 2016; Giles et al. 2017) and oilseed rape can induce the dissolution of phlogopite mica, and the subsequent release of interlayer K, by rhizosphere acidification more effectively than Italian ryegrass (*Lolium multiflorum* Lam.; Hinsinger 2013).

Root exudates can also have a profound effect on the dissolution of feldspars and micas and, therefore, on the availability of nonexchangeable (structural and interlayer, respectively) soil K to plants. The composition of root exudates differs between plant species, which affects their ability to acquire nonexchangeable K (Hinsinger 2013; Giles et al. 2017; Hinsinger et al. 2017). Root exudates can also change during plant development and in response to environmental factors (Neumann and Römheld 2012; Kuijken et al. 2015; Giles et al. 2017). The exudation of carboxylates, such as citrate, malate, and oxalate, promotes the dissolution of feldspars and micas by complexing cations contained in their crystal lattice (Marchi et al. 2012; Chap. 4). Plant species vary greatly in the amounts and diversity of carboxylates their roots release into the rhizosphere (Hinsinger 2013; Zörb et al. 2014; Bell et al. 2017; Rengel and Djalovic 2017). Roots of Caryophyllales, including grain amaranths and beets, can access nonexchangeable K by exuding copious amounts of carboxylates (Wang et al. 2011). Roots of white lupin (*Lupinus albus* L.), and other species forming cluster roots, exude considerable quantities of both citrate and malate, as do many brassica crops (White et al. 2005; Hinsinger 2013). Greater acquisition of nonexchangeable K by *Cucurbita pepo* subsp. *pepo* than *C. pepo* subsp. *ovifera* was attributed to the greater citrate content in root exudates of subsp. *pepo* (Gent et al. 2005), while the dominant carboxylate in root exudates of K-deficient crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) appears to be malate (Henry et al. 2007). By contrast, solanaceous crops generally release carboxylates such as succinate, rather than citrate, into the rhizosphere and are relatively ineffective in acquiring nonexchangeable K from the soil (Steingrobe and Claassen 2000; White et al. 2005; White 2013). Legumes, such as alfalfa and pea, are also relatively ineffective in acquiring nonexchangeable K from the soil (Høgh-Jensen and Pedersen 2003). In addition to carboxylates, roots of different species exude a variety of amino acids and phytosiderophores, proteins, including enzymes, sugars, and polysaccharides (mucilage), flavonoids, and phenolic compounds (e.g., ferulic acid, p-coumaric acid, and cinnamic acid) into the rhizosphere (Neumann and Römheld 2012), although it is not yet known whether these compounds facilitate the acquisition of K by plants.

5.2.2 *Differences in KUtE Between Plant Species*

Plant species also differ in their ability to utilize the K they have acquired for growth and yield formation (White 2013). Most crops have a high K demand, which is ultimately set by their growth rate and, most often, by the nitrogen supply that generally determines their growth rate (Fageria 2009, 2015a; White and Greenwood 2013). The physiological K requirement of a plant is determined by its critical tissue K concentration, defined as the concentration at which the plant achieves 90% of its maximum growth, and its growth rate (White 2013). The tissue K concentration at which K deficiency symptoms appear in leaves is generally lower in cereals and grasses than in legumes and other eudicots, which reflects their lower physiological K requirements (Johnson 1973; Greenwood et al. 1980; Brennan and Bolland 2004, 2007; Römheld 2012; White 2013). Similarly, seed K concentrations are generally lower in cereals (3–5 g K kg^{-1} grain) than in oilseeds (5–10 g K kg^{-1} grain) and legumes (10–20 g K kg^{-1} grain; Fig. 5.4). Since crops generally have large harvest indices, achieving appropriate K concentrations in seed has significant implications for the agronomic use of K fertilizers in crop production.

In general, physiological K utilization efficiency can be improved by (1) reducing vacuolar K concentration while maintaining an appropriate cytoplasmic K concentration, either by anatomical adaptations or by greater substitution of K with other solutes in the vacuole, and (2) redistributing K from older to younger tissues to maintain growth and photosynthesis (Rengel and Damon 2008; Wakeel et al. 2011;

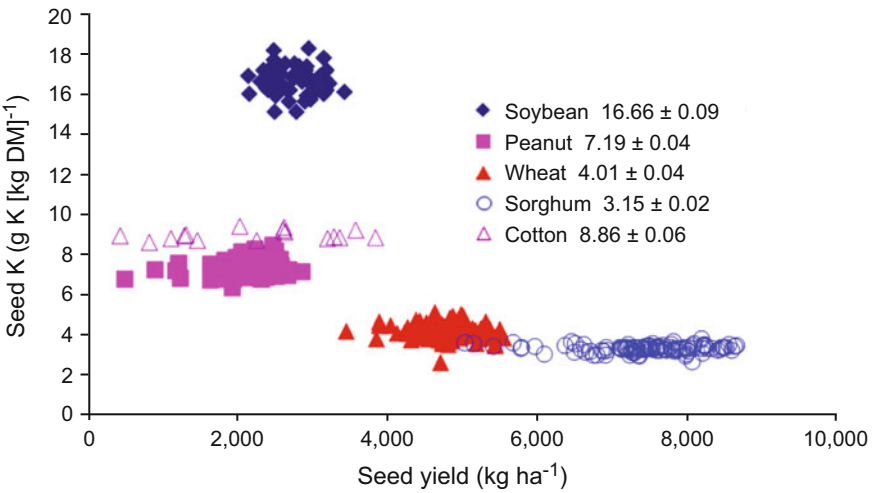

Fig. 5.4 Relationships between crop yield (as determined by variation in soil K status) and the K concentration in grains harvested from soybean, peanut, wheat, sorghum, and cotton crops grown on an Oxisol soil at Kingaroy, SE Queensland, Australia (Bell et al. unpublished). Data for each species were obtained over 2–3 growing seasons. The data illustrate the consistency of grain K concentration within each plant species irrespective of either yield or leaf K concentration (not shown)

White 2013; Maillard et al. 2015). The ability to substitute K with sodium (Na) in the vacuole is important for efficient K utilization in many, but not all, plant species and is particularly evident in species adapted to soils with low K availability and in natrophilic species, such as sugar beet (Wakeel et al. 2011; Gattward et al. 2012; Battie-Laclau et al. 2014; Erel et al. 2014; Zörb et al. 2014; White et al. 2017). About 60% of the K in cells of sugar beet can be replaced by Na, whereas less than 15% of the K in cells of wheat can be replaced (Zörb et al. 2014). The ability to retranslocate K from senescing tissues also differs between plant species (Hocking and Pate 1977; Milla et al. 2005; Maillard et al. 2015). In general, plant species with greater KUtE can maintain their water relations, photosynthetic activity, and harvest index when grown in environments with a low K supply (Rengel and Damon 2008; White 2013).

5.3 Differences in Potassium Uptake and Utilization Within Crop Species

Differences in growth and yield responses to K supply, KUE, KUpE, and KUtE have been reported among genotypes of many crop species (Baligar et al. 2001; Rengel and Damon 2008; Fageria 2009, 2015a; Römheld and Kirkby 2010; White 2013; Zörb et al. 2014; White and Bell 2017). Although variation in KUE has been correlated with variation in both KUpE and KUtE, depending upon plant species and growth conditions, it is most often correlated with KUpE in crop species (Rengel and Damon 2008; Fageria 2009; White 2013).

5.3.1 Differences in KUpE Within Plant Species

Variation in KUpE has been observed among genotypes of barley (Pettersson and Jensén 1983; Siddiqi and Glass 1983a; Wu et al. 2011; Kuzmanova et al. 2014; White et al. 2016), wheat (Zhang et al. 1999; Damon and Rengel 2007; Damon et al. 2011), wild oats (*Avena fatua* L.; Siddiqi et al. 1987), rice (*Oryza sativa* L.; Yang et al. 2004; Fageria 2009, 2015b; Liu et al. 2009; Fageria et al. 2010, 2013; Sanes et al. 2013; Fageria and dos Santos 2015), maize (Feil et al. 1992; Allan et al. 1998; Nawaz et al. 2006; Ning et al. 2013), common bean (*Phaseolus vulgaris* L.; Fageria et al. 2001, 2015; Fageria and Melo 2014), faba bean (*Vicia faba* L.; Stelling et al. 1996), soybean (*Glycine max* (L.) Merr.; Moreira et al. 2015), lupin (*Lupinus angustifolius* L.; Brennan and Bolland 2004), canola (Damon et al. 2007; Lu et al. 2016), *Brassica oleracea* L. (White et al. 2010), Indian mustard (*Brassica juncea* (L.) Czern.; Shi et al. 2004), cassava (*Manihot esculenta* Crantz; Spear et al. 1978b), sweet potato (*Ipomoea batatas* L.; George et al. 2002; Wang et al. 2015a), tomato (Chen and Gabelman 1995, 2000; Sánchez-Rodríguez et al. 2010), potato (*Solanum tuberosum* L.; Trehan 2005), cotton (*Gossypium hirsutum* L.; Ali et al. 2006; Zhang

et al. 2007; Yang et al. 2011; Chen et al. 2014; Zia-ul-hassan et al. 2014; Rochester and Constable 2015) and watermelon (*Citrullus lanatus* (Thunb.) Matsum. and Nakai; Fan et al. 2013). The same traits that contribute to differences in KUpE between plant species also contribute to differences in KUpE among genotypes within plant species. These include differences in (1) the capacity of their root cells to take up K^+ at low rhizosphere K^+ concentrations, (2) the ability of their root systems to proliferate and exploit the soil volume effectively, and (3) the ability of their roots to induce the release of nonexchangeable K from the soil, depending upon the crop species and the environment in which they are grown.

5.3.1.1 Kinetics of Potassium Uptake

The rate of K uptake by roots is determined by both the cellular capacity for K uptake, the affinity for K in the rhizosphere solution, and the K concentration in the rhizosphere solution at K flux equilibrium (White 2013; Hinsinger et al. 2017). Differences in the capacity for K uptake of roots have been observed among genotypes of many crops (White 2013; Rengel and Djalovic 2017) and, when assayed at low K^+ concentrations in the rhizosphere solution, genotypes of, for example, barley (Siddiqi and Glass 1983b), Chinese cabbage (*Brassica rapa* L.; Li et al. 2015), tomato (Chen and Gabelman 1995, 2000) and potato (Trehan 2005) with greatest root K uptake capacities often having the greatest KUpE.

5.3.1.2 Root System Investment and Architecture

In general, the ability of a root system to forage the soil is related to its length and its direct interaction with the rhizosphere, which is conferred by its surface area (White 2013). There is considerable variation among genotypes of crop species in the length and architecture of their root system, the distribution of roots in the soil, the length/biomass quotients of root types, and the abundance, length, and longevity of root hairs (e.g., White et al. 2005; Gahoonia et al. 2006, 2007; Hammond et al. 2009; Wishart et al. 2013; Adu et al. 2014; Atkinson et al. 2015; Lynch 2015; Yu et al. 2015; Thomas et al. 2016; Chen et al. 2017; Erel et al. 2017).

Chromosomal loci (QTL) affecting these traits in seedlings have been identified (Lynch 2007; White et al. 2013; Atkinson et al. 2015; Kuijken et al. 2015). When compared at low K supply, maize (Minjian et al. 2007), rice (Jia et al. 2008; Sanes et al. 2013), wheat (Ehdaie et al. 2010), potato (Trehan 2005), tomato (Chen and Gabelman 1995, 2000), Chinese cabbage (Li et al. 2015), and cotton (Yang et al. 2011; Zia-ul-hassan and Arshad 2011) genotypes with larger roots have greater KUpE, and often faster growth and greater yields, than other genotypes. Similarly, enlarging the root system of rice by overexpressing the WUSCHEL-related homeobox gene WOX11 increased both K uptake and grain yield when K availability was low (Chen et al. 2015). Although there was a weak correlation between KUpE and root length among different genotypes of lentil (*Lens culinaris* Medikus), there was a

stronger correlation between KUpE and the length of root hairs (Gahoonia et al. 2006). A strong correlation between KUpE and the abundance and length of root hairs was also observed among genotypes of chickpea (*Cicer arietinum* L.; Gahoonia et al. 2007) and cotton (Tao et al. 2012). Other aspects of root architecture can also contribute to differences in KUpE among genotypes of a particular species. For example, genotypes of ramie (*Boehmeria nivea* (L.) Gaudich.) whose root systems comprise a large proportion of thin roots often have greater KUpE than other genotypes (Cui and Li 2000), although this phenomenon was not observed in Chinese cabbage (Li et al. 2015).

5.3.1.3 Root Exudates

When the K uptake capacity of root cells exceeds the rate at which K is supplied to the root, K uptake is determined by the rate at which K can be replenished at the root surface. This is determined both by the movement of solution to the root surface, which is often governed by transpiration, and by the ability of the plant to mobilize nonexchangeable K from the soil, which is influenced by root exudates (White 2013).

There is considerable variation between genotypes within plant species in both the composition and quantity of root exudates that can induce the release of nonexchangeable K from the soil. For example, genotypes of barley, wheat, maize, and sorghum vary greatly in their exudation of malate and citrate into the rhizosphere (e.g., Ryan et al. 2011; Giles et al. 2017), root exudates of *Cucurbita pepo* subsp. *pepo* contain more citrate than those of *Cucurbita pepo* subsp. *ovifera* (Gent et al. 2005), canola genotypes differ in the quantity and diversity of carboxylates they release into the rhizosphere (Akhtar et al. 2006, 2008) and in their ability to acquire nonexchangeable K (Shi et al. 2004), and genotypes of potato with greater KUpE mobilize more nonexchangeable K than other genotypes (Trehan 2005).

5.3.2 Differences in KUtE Within Crop Species

Variation in KUtE has been observed among genotypes of barley (Pettersson and Jensén 1983; Wu et al. 2011; Kuzmanova et al. 2014; White et al. 2016), wheat (Woodend and Glass 1993; Zhang et al. 1999; Baligar et al. 2001; Damon and Rengel 2007; Damon et al. 2011; Moriconi et al. 2012), wild oats (Siddiqi et al. 1987), rice (Yang et al. 2003, 2004; Fageria 2009, 2015b; Liu et al. 2009; Fageria et al. 2010, 2013; Zhang et al. 2013; Fageria and dos Santos 2015), maize (Feil et al. 1992; Baligar et al. 2001; Nawaz et al. 2006), sorghum (Baligar et al. 2001), common bean (Fageria et al. 2001, 2015; Fageria and Melo 2014), faba bean (Stelling et al. 1996), soybean (Moreira et al. 2015), alfalfa (Baligar et al. 2001), lupin (Brennan and Bolland 2004), canola (Damon et al. 2007; Lu et al. 2016), *Brassica oleracea* (White et al. 2010), Chinese cabbage (Wu et al. 2008), Indian

mustard (Shi et al. 2004), spinach (*Spinacia oleracea* L.; Grusak and Cakmak 2005), cassava (Spear et al. 1978a, b), sweet potato (George et al. 2002; Wang et al. 2015a), tomato (Chen and Gabelman 1995), potato (Trehan 2005), cotton (Ali et al. 2006; Zhang et al. 2007; Yang et al. 2011; Chen et al. 2014; Zia-ul-hassan et al. 2014; Rochester and Constable 2015) and watermelon (Fan et al. 2013). However, it is noteworthy that KUtE for vegetative growth does not always correlate with KUtE for crop yield. The same traits that contribute to differences in KUtE between plant species also contribute to differences in KUtE among genotypes of a particular species.

5.3.2.1 Partitioning of Potassium Within the Cell and Its Substitution with Other Ions

In metabolically active compartments, such as the cytosol, mitochondria, and plastids, K^+ concentrations must be maintained at about 100 mM to ensure protein function and provide charge balance (White and Karley 2010). When K is in limited supply, these compartments take precedence and cellular K can be reduced by substituting vacuolar K with other elements. Thus, it has been observed that genotypes of barley that are less susceptible to K deficiency symptoms partition K more effectively from the vacuole to the cytoplasm of root cells at low K supply (Memon et al. 1985), and the ability of tomato (Figdore et al. 1989) and maize (Moriconi et al. 2012) genotypes to grow in Na-rich, K-limiting conditions correlates with their ability to substitute Na for K as a vacuolar osmoticum.

5.3.2.2 Partitioning and Redistribution of Potassium Within the Plant

Potassium is required for stomatal opening, photosynthetic performance, and the movement of photosynthates to developing tissues (White and Karley 2010). The ability to maintain gas exchange, photosynthesis, and phloem translocation to developing tissues under conditions of restricted K supply requires effective redistribution of K from older to younger tissues. Thus, the redistribution of K within the plant can contribute significantly to KUtE. For example, the ability to redistribute K from older to younger leaves has been found to correlate with greater KUtE among genotypes of cassava (Spear et al. 1978b) and rice (Yang et al. 2004) and the ability to maintain photosynthesis at a low K supply correlates with better growth among soybean genotypes (Wang et al. 2015b). Differences in harvest index (the ability to translocate carbon into the harvested tissue), which is a component trait of KUtE, contribute to variation in yield among rice (Yang et al. 2003, 2004; Fageria et al. 2010; Zhang et al. 2013), wheat (Woodend and Glass 1993; Zhang et al. 1999; Damon and Rengel 2007), common bean (Fageria et al. 2001), faba bean (Stelling et al. 1996), canola (Rose et al. 2007), sweet potato (George et al. 2002) and cotton (Rochester and Constable 2015) genotypes, especially when grown with a low K supply.

5.3.2.3 Partitioning of Resources into the Economic Product

Potassium is required for electroneutrality in both the loading of sucrose and the transport of anions in the phloem (White and Karley 2010). Although there are considerable differences among genotypes of a crop species, the seed K concentration of a particular genotype is often relatively insensitive to plant K nutrition (Fig. 5.4). However, tuber K concentration does vary with plant K nutrition (White et al. 2009). The relationships between KUE, KUtE, and K partitioning to edible portions are currently unknown. However, given that K is essential for animal nutrition and there is substantial interest in the links between plant and human nutrition (White 2016), these relationships should be investigated.

5.4 Breeding Crops for Greater Agronomic Potassium Use Efficiency

Breeding for greater KUE relies upon (1) useful variation in component traits within germplasm resources, (2) the ability to identify beneficial traits in large germplasm collections, either through phenotypic or genetic analyses, and (3) the ability to incorporate beneficial traits into commercial varieties or locally adapted germplasm (Rengel and Damon 2008; White 2013; White and Bell 2017).

There appears to be sufficient, heritable genetic variation within crop species to breed for genotypes with greater KUE, KUpE, and KUtE (White 2013). However, these traits are controlled by multiple chromosomal loci (QTL) and strong interactions between genotype and environment can occur (e.g., White et al. 2010; Guo et al. 2012; Genc et al. 2013; Gong et al. 2015). This implies that breeding programs should incorporate beneficial alleles of several genes to improve KUE and consider carefully the conditions under which genotypes are screened and cultivated. Breeding programs have generally focused on increasing yield under current management practices, which, although resulting in greater KUE under current management practices, does not address the needs of reduced-input agriculture. This omission must be redressed in the future.

To breed for greater KUE, breeding programs must be able to screen many genotypes for variation in KUE, KUpE, or KUtE or to identify genetic variation linked to these traits (Rengel and Damon 2008; White and Bell 2017). A successful breeding program also requires the ability to characterize the relationships between K supply, plant K content, and yield formation in a variety of environments to reveal interactions between genotype, management, and environmental conditions. In principle, the required data can be obtained from simple measurements of the response of yield and K content to varying K fertilizer application at several well-chosen sites across several years (White and Bell 2017). This effort can be facilitated by reducing the number of treatments required to estimate the responses of KUE, KUpE, and KUtE to management and fertilizer practices using crop modelling

approaches or theoretical considerations (Moriconi and Santa-María 2013; Santa-María et al. 2015; White et al. 2016) and developing techniques to estimate crop biomass and K content that are less costly and labor intensive than conventional mineral analyses (White and Bell 2017). An alternative approach is to screen for morphological, physiological, or biochemical traits associated with greater KUpE and KUtE using high-throughput laboratory or glasshouse systems (Downie et al. 2015; Kuijken et al. 2015).

Chromosomal loci influencing KUpE, KUtE, shoot K concentration, or biomass production at low K supply have been identified in a few model species, such as arabidopsis (e.g., Harada and Leigh 2006; Ghandilyan et al. 2009; Kanter et al. 2010; Prinzenberg et al. 2010), and in several crops, including rice (Wu et al. 1998; Koyama et al. 2001; Lin et al. 2004; Cheng et al. 2012; Wang et al. 2012; Miyamoto et al. 2012; Fang et al. 2015; Khan et al. 2015), wheat (Genc et al. 2010, 2013; Guo et al. 2012; Kong et al. 2013; Zhao et al. 2014; Gong et al. 2015), barley (Nguyen et al. 2013a, b), maize (Zdunić et al. 2014), miscanthus (*Miscanthus sinensis* Andersson; Atienza et al. 2003), tomato (Villalta et al. 2008; Asins et al. 2013), barrel medic (*Medicago truncatula* Gaertn.; Arraouadi et al. 2012), *Brassica oleracea* (White et al. 2010), apple (*Malus pumila* Miller; Fazio et al. 2013), and cotton (Liu et al. 2015). However, few genes underpinning these QTL have been identified. Nevertheless, it has been reported that genes encoding K^+ transporters, such as AtAKT1, AtHAK5, AtKUP9, AtTPK1, AtCNGC1, and AtSKOR, are located within QTL affecting shoot K concentration in arabidopsis (Harada and Leigh 2006; Kanter et al. 2010) and genes encoding homologs of the arabidopsis K^+ transporters AtKUP9, AtAKT2, AtKAT2, and AtTPK3 occur within a QTL affecting shoot K concentration in *Brassica oleracea* (White et al. 2010). Similarly, genes affecting shoot K concentration located within a QTL on chromosome 14 of cotton include numerous cation transporters, such as AKT2/3 and a Na^+/H^+-antiporter (Liu et al. 2015). In rice, the gene *OsHKT1;5* (*OsHKT8*), which encodes a Na^+ transporter expressed predominantly in the parenchyma cells surrounding the xylem, underpins the locus SKC1 that affects shoot K concentration under saline conditions (Ren et al. 2005). Similarly, HvHKT1;5, TmHKT1;5-A, and TaHKT1:5-D have been implicated in the control of shoot Na and K concentrations in barley and wheat (Munns et al. 2012; Nguyen et al. 2013a) and SlHKT1;1 and SlHKT1;2 have been implicated in the control of shoot Na and K concentrations in tomato (Asins et al. 2013).

5.5 Conclusions

Many terms have been used to define aspects of K use efficiency in plants (Table 5.1). Agronomic K use efficiency (KUE) is defined based on crop yield and is equal to the product of K uptake efficiency (KUpE) and K utilization efficiency (KUtE). Differences in KUE between plant species, and between genotypes within a species, reflect differences in their KUpE and KUtE. In crop species, KUE is most often correlated with KUpE.

Differences in KUpE have been attributed to differences in (1) the capacity of root cells to take up K^+ at low rhizosphere K^+ concentrations, (2) the ability of root systems to exploit the soil volume effectively, and (3) the release of exudates into the rhizosphere that promote the release of nonexchangeable K from the soil. Differences in KUtE have been attributed to differences in (1) the ability to reduce cellular K concentration while maintaining appropriate K concentrations in metabolically active compartments, either by anatomical adaptations or by greater substitution of K with other solutes in the vacuole, and (2) the ability to redistribute K from older to younger tissues and, thereby, maintain growth and photosynthetic capacity. There is sufficient heritable variation in both KUpE and KUtE to develop crops with greater KUE.

Given that KUpE and KUtE are polygenic and there are strong interactions between genotype and environment, breeding programs should include beneficial alleles of several genes and consider carefully the conditions under which genotypes are developed and deployed. It is likely that the full economic benefit of genotypes with greater KUE will require complementary agricultural management practices. Combining genetic and agronomic strategies to make better use of K fertilizers in agriculture would reduce fertilizer costs, protect the environment, and slow the exhaustion of nonrenewable resources.

Acknowledgment The contribution of PJW to this work was supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government.

References

Adu MO, Chatot A, Wiesel L, Bennett MJ, Broadley MR, White PJ, Dupuy LX (2014) A scanner system for high-resolution quantification of variation in root growth dynamics of *Brassica rapa* genotypes. J Exp Bot 65:2039–2048. https://doi.org/10.1093/jxb/eru048

Akhtar MS, Oki Y, Adachi T, Murata Y, Khan MHR (2006) Phosphorus starvation induced root-mediated pH changes in solubilization and acquisition of sparingly soluble P sources and organic acids exudation by Brassica cultivars. Soil Sci Plant Nutr 52:623–633. https://doi.org/10.1111/j.1747-0765.2006.00082.x

Akhtar MS, Oki Y, Adachi T (2008) Genetic variability in phosphorus acquisition and utilization efficiency from sparingly soluble P-sources by *Brassica* cultivars under P-stress environment. J Agron Crop Sci 194:380–392. https://doi.org/10.1111/j.1439-037X.2008.00326.x

Ali L, Rahmatullah, Ranjha AM, Aziz T, Maqsood MA, Ashraf M (2006) Differential potassium requirement and its substitution by sodium in cotton genotypes. Pak J Agric Sci 43:108–113

Allan DL, Rehm GW, Oldham JL (1998) Root system interactions with potassium management in corn. In: Oosterhuis D, Berkowitz G (eds) Frontiers in potassium nutrition: new perspectives on the effects of potassium on physiology of plants. Potash and Phosphate Institute, Norcross, pp 111–116

Arraouadi S, Badri M, Abdelly C, Huguet T, Aouani ME (2012) QTL mapping of physiological traits associated with salt tolerance in *Medicago truncatula* recombinant inbred lines. Genomics 99:118–125. https://doi.org/10.1016/j.ygeno.2011.11.005

Asher CJ, Ozanne PG (1967) Growth and potassium content of plants in solution cultures maintained at constant potassium concentrations. Soil Sci 103:155–161

Asins MJ, Villalta I, Aly MM, Olias R, De Morales PA, Huertas R, Li J, Jaime-Perez N, Haro R, Raga V, Carbonell EA, Belver A (2013) Two closely linked tomato HKT coding genes are positional candidates for the major tomato QTL involved in Na^+/K^+ homeostasis. Plant Cell Environ 36:1171–1191. https://doi.org/10.1111/pce.12051

Atienza SG, Satovic Z, Petersen KK, Dolstra O, Martín A (2003) Identification of QTLs influencing combustion quality in *Miscanthus sinensis* Anderss. II. Chlorine and potassium content. Theor Appl Genet 107:857–863. https://doi.org/10.1007/s00122-003-1218-z

Atkinson JA, Wingen LU, Griffiths M, Pound MP, Gaju O, Foulkes MJ, Le Gouis J, Griffiths S, Bennett MJ, King J (2015) Phenotyping pipeline reveals major seedling root growth QTL in hexaploid wheat. J Exp Bot 66:2281–2292. https://doi.org/10.1093/jxb/erv006

Baligar VC, Fageria NK, He ZL (2001) Nutrient use efficiency in plants. Commun Soil Sci Plant Anal 32:921–950. https://doi.org/10.1007/978-81-322-2169-2_1

Battie-Laclau P, Laclau J-P, Beri C, Mietton L, Muniz MRA, Arenque BC, Piccolo MDC, Jordan-Meille L, Bouillet JP, Nouvellon Y (2014) Photosynthetic and anatomical responses of *Eucalyptus grandis* leaves to potassium and sodium supply in a field experiment. Plant Cell Environ 37:70–81. https://doi.org/10.1111/pce.12131

Bell MJ, Moody P, Thompson M, Guppy C, Mallarino AP, Goulding K (2017) Improving potassium rate recommendations by recognizing soil potassium pools with dissimilar bioavailability. In: Murrell TS, Mikkelsen RL (eds) Proceedings for the frontiers of potassium science conference, 25–27 January 2017, Rome, Italy. International Plant Nutrition Institute, Peachtree Corners, pp 239–248. https://www.apni.net/k-frontiers/. Accessed 29 May 2020

Brennan RF, Bell MJ (2013) Soil potassium-crop response calibration relationships and criteria for field crops grown in Australia. Crop Pasture Sci 64:514–522. https://doi.org/10.1071/CP13006

Brennan RF, Bolland MDA (2004) Lupin takes up less potassium but uses the potassium more effectively to produce shoots than canola and wheat. Aust J Exp Agric 44:309–319. https://doi.org/10.1071/EA02232

Brennan RF, Bolland MDA (2007) Comparing the potassium requirements of canola and wheat. Aust J Agric Res 58:359–366. https://doi.org/10.1071/AR06244

Broadley MR, Bowen HC, Cotterill HL, Hammond JP, Meacham MC, Mead A, White PJ (2004) Phylogenetic variation in the shoot mineral concentration of angiosperms. J Exp Bot 55:321–336. https://doi.org/10.1093/jxb/erh002

Chen J, Gabelman WH (1995) Isolation of tomato strains varying in potassium acquisition using a sand-zeolite culture system. Plant Soil 176:65–70. https://doi.org/10.1007/BF00017676

Chen J, Gabelman WH (2000) Morphological and physiological characteristics of tomato roots associated with potassium-acquisition efficiency. Sci Hortic 83:213–225. https://doi.org/10.1016/S0304-4238(99)00079-5

Chen Y, Wen Y, Wang J, Zhang X, Chen D (2014) Cotton potassium uptake and use efficiency vary with potassium application rates and soil potassium nutrition levels. J Food Agric Environ 12:221–227

Chen G, Feng H, Hu Q, Qu H, Chen A, Yu L, Xu G (2015) Improving rice tolerance to potassium deficiency by enhancing OsHAK16p:WOX11-controlled root development. Plant Biotechnol J 13:833–848. https://doi.org/10.1111/pbi.12320

Chen Y, Ghanem ME, Siddique KHM (2017) Characterising root trait variability in chickpea (*Cicer arietinum* L.) germplasm. J Exp Bot 68:1987–1999. https://doi.org/10.1093/jxb/erw368

Cheng L, Wang Y, Meng L, Hu X, Cui Y, Sun Y, Zhu L, Ali J, Xu J, Li Z (2012) Identification of salt-tolerant QTLs with strong genetic background effect using two sets of reciprocal introgression lines in rice. Genome 55:45–55. https://doi.org/10.1139/g11-075

Coskun D, Britto DT, Li M, Oh S, Kronzucker HJ (2013) Capacity and plasticity of potassium channels and high-affinity transporters in roots of barley and Arabidopsis. Plant Physiol 162:496–511. https://doi.org/10.1104/pp.113.215913

Cui G, Li Z (2000) Relationship between potassium absorption and root parameters of different genotypes of ramie. Res Agric Modernization 21:371–375

Damon PM, Rengel Z (2007) Wheat genotypes differ in potassium efficiency under glasshouse and field conditions. Aust J Agric Res 58:816–825. https://doi.org/10.1071/AR06402

Damon PM, Osborne LD, Rengel Z (2007) Canola genotypes differ in potassium efficiency during vegetative growth. Euphytica 156:387–397. https://doi.org/10.1007/s10681-007-9388-4

Damon PM, Ma QF, Rengel Z (2011) Wheat genotypes differ in potassium accumulation and osmotic adjustment under drought stress. Crop Pasture Sci 62:550–555. https://doi.org/10.1071/CP11071

Downie HF, Adu MO, Schmidt S, Otten W, Dupuy LX, White PJ, Valentine TA (2015) Challenges and opportunities for quantifying roots and rhizosphere interactions through imaging and image analysis. Plant Cell Environ 38:1213–1232. https://doi.org/10.1111/pce.12448

Ehdaie B, Merhaut DJ, Ahmadian S, Hoops AC, Khuong T, Layne AP, Waines JG (2010) Root system size influences water-nutrient uptake and nitrate leaching potential in wheat. J Agron Crop Sci 196:455–466. https://doi.org/10.1111/j.1439-037X.2010.00433.x

El Dessougi H, Claassen N, Steingrobe B (2002) Potassium efficiency mechanisms of wheat, barley, and sugar beet grown on a K fixing soil under controlled conditions. J Plant Nutr Soil Sci 165:732–737. https://doi.org/10.1002/jpln.200290011

El Dessougi HI, Claassen N, Steingrobe B (2010) Potassium efficiency of different crops grown on a sandy soil under controlled conditions. Univ Khartoum J Agric Sci 18:310–334

Erel R, Ben-Gal A, Dag A, Schwartz A, Yermiyahu U (2014) Sodium replacement of potassium in physiological processes of olive trees (var. Barnea) as affected by drought. Tree Physiol 34:1102–1117. https://doi.org/10.1093/treephys/tpu081

Erel R, Bérard A, Capowiez L, Doussan C, Arnal D, Souche G, Gavaland A, Fritz C, Visser EJW, Salvi S, Le Marié C, Hund A, Hinsinger P (2017) Soil type determines how root and rhizosphere traits relate to phosphorus acquisition in field-grown maize genotypes. Plant Soil 412:115–132. https://doi.org/10.1007/s11104-016-3127-3

Fageria NK (2009) The use of nutrients in crop plants. CRC Press, Boca Raton

Fageria NK (2015a) Potassium. In: Barker AV, Pilbeam DJ (eds) A handbook of plant nutrition, 2nd edn. CRC Press, Boca Raton, pp 127–163

Fageria NK (2015b) Lowland rice genotypes evaluation for potassium-use efficiency. Commun Soil Sci Plant Anal 46:1628–1635. https://doi.org/10.1081/PLN-120015539

Fageria NK, dos Santos AB (2015) Agronomic evaluation of lowland rice genotypes for potassium-use efficiency. Commun Soil Sci Plant Anal 46:1327–1344. https://doi.org/10.1080/01904167.2014.911889

Fageria NK, Melo LC (2014) Agronomic evaluation of dry bean genotypes for potassium use efficiency. J Plant Nutr 37:1899–1912. https://doi.org/10.1080/01904167.2014.911889

Fageria NK, Barbosa Filho MP, da Costa JGC (2001) Potassium-use efficiency in common bean genotypes. J Plant Nutr 24:1937–1945. https://doi.org/10.1081/PLN-100107605

Fageria NK, dos Santos AB, de Moraes MF (2010) Yield, potassium uptake, and use efficiency in upland rice genotypes. Commun Soil Sci Plant Anal 41:2676–2684. https://doi.org/10.1080/00103624.2010.517882

Fageria NK, Moreira A, Ferreira EPB, Knupp AM (2013) Potassium-use efficiency in upland rice genotypes. Commun Soil Sci Plant Anal 44:2656–2665. https://doi.org/10.1080/00103624.2013.813031

Fageria NK, Melo LC, Knupp AM (2015) Dry bean genotype evaluation for potassium-use efficiency. Commun Soil Sci Plant Anal 46:1061–1075. https://doi.org/10.1080/00103624.2014.981637

Fan M, Bie Z, Xie H, Zhang F, Zhao S, Zhang H (2013) Genotypic variation for potassium efficiency in wild and domesticated watermelons under ample and limited potassium supply. J Plant Nutr Soil Sci 176:466–473. https://doi.org/10.1002/jpln.201200007

Fang Y, Wu W, Zhang X, Jiang H, Lu W, Pan J, Hu J, Guo L, Zeng D, Xue D (2015) Identification of quantitative trait loci associated with tolerance to low potassium and related ions concentrations at seedling stage in rice (*Oryza sativa* L.). Plant Growth Regul 77:157–166. https://doi.org/10.1007/s10725-015-0047-9

Fazio G, Kviklys D, Grusak MA, Robinson T (2013) Phenotypic diversity and QTL mapping of absorption and translocation of nutrients by apple rootstocks. Asp Appl Biol 119:37–50

Feil B, Thiraporn R, Geisler G, Stamp P (1992) Yield, development and nutrient efficiency of temperate and tropical maize germplasm in the tropical lowlands. II. Uptake and redistribution of nitrogen, phosphorus and potassium. Maydica 37:199–207

Figdore SS, Gabelman WH, Gerloff GC (1989) Inheritance of potassium efficiency, sodium substitution capacity, and sodium accumulation in tomatoes grown under low-potassium stress. J Am Soc Hortic Sci 114:322–327

Gahoonia TS, Ali O, Sarker A, Nielsen NE, Rahman MM (2006) Genetic variation in root traits and nutrient acquisition of lentil genotypes. J Plant Nutr 29:643–655. https://doi.org/10.1080/01904160600564378

Gahoonia TS, Rawshan A, Malhotra RS, Jahoor A, Rahman MM (2007) Variation in root morphological and physiological traits and nutrient uptake of chickpea genotypes. J Plant Nutr 30:829–841. https://doi.org/10.1080/15226510701373213

Gattward JN, Almeida A-AF, Souza JO, Gomes FP, Kronzucker HJ (2012) Sodium-potassium synergism in *Theobroma cacao*: stimulation of photosynthesis, water-use efficiency and mineral nutrition. Physiol Plant 146:350–362. https://doi.org/10.1111/j.1399-3054.2012.01621.x

Genc Y, Oldach K, Verbyla AP, Lott G, Hassan M, Tester M, Wallworth H, McDonald GK (2010) Sodium exclusion QTL associated with improved seedling growth in bread wheat under salinity stress. Theor Appl Genet 121:877–894. https://doi.org/10.1007/s00122-010-1357-y

Genc Y, Oldach K, Gogel B, Wallwork H, McDonald GK, Smith AB (2013) Quantitative trait loci for agronomical and physiological traits for a bread wheat population grown in environments with a range of salinity levels. Mol Breed 32:39–59. https://doi.org/10.1007/s11032-013-9851-y

Gent MPN, Parrish ZD, White JC (2005) Nutrient uptake among subspecies of *Cucurbita pepo* L. is related to exudation of citric acid. J Am Soc Hortic Sci 130:782–788. https://doi.org/10.21273/JASHS.130.5.782

George MS, Lu G, Zhou W (2002) Genotypic variation for potassium uptake and utilization efficiency in sweet potato (*Ipomoea batatas* L.). Field Crops Res 77:7–15. https://doi.org/10.1016/S0378-4290(02)00043-6

Ghandilyan A, Ilk N, Hanhart C, Mbengue M, Barboza L, Schat H, Koornneef M, El-Lithy M, Vreugdenhil D, Reymond M, Aarts MGM (2009) A strong effect of growth medium and organ type on the identification of QTLs for phytate and mineral concentrations in three *Arabidopsis thaliana* RIL populations. J Exp Bot 60:1409–1425. https://doi.org/10.1093/jxb/erp084

Giles CD, Brown LK, Adu MO, Mezeli MM, Sandral GA, Simpson RJ, Wendler R, Shand CA, Menezes-Blackburn D, Darch T, Stutter MI, Lumsdon DG, Zhang H, Blackwell MSA, Wearing C, Cooper P, Haygarth PM, George TS (2017) Response-based selection of barley cultivars and legume species for complementarity: root morphology and exudation in relation to nutrient source. Plant Sci 255:12–28. https://doi.org/10.1016/j.plantsci.2016.11.002

Gong X-P, Liang X, Guo Y, Wu C-H, Zhao Y, Li X-H, Li S-S, Kong F-M (2015) Quantitative trait locus mapping for potassium use efficiency traits at the seedling stage in wheat under different nitrogen and phosphorus treatments. Crop Sci 55:2690–2700. https://doi.org/10.2135/cropsci2014.10.0711

Grant CA, Derksen DA, Blackshaw RE, Entz T, Janzen HH (2007) Differential response of weed and crop species to potassium and sulphur fertilizers. Can J Plant Sci 87:293–296. https://doi.org/10.4141/P06-138

Greenwood DJ, Cleaver TJ, Turner MK, Hunt J, Niendorf KB, Loquens SMH (1980) Comparison of the effects of potassium fertilizer on the yield, potassium content and quality of 22 different vegetables and agricultural crops. J Agric Sci 95:441–456. https://doi.org/10.1017/S0021859600039496

Gregory PJ (2006) Plant roots. Growth, activity and interaction with soils. Blackwell, Oxford. https://doi.org/10.1002/9780470995563.fmatter

Grusak MA, Cakmak I (2005) Methods to improve the crop delivery of minerals to humans and livestock. In: Broadley MR, White PJ (eds) Plant nutritional genomics. Blackwell, Oxford, pp 265–286

Guo Y, Kong F-M, Xu Y-F, Zhao Y, Liang X, Wang Y-Y, An D-G, Li S-S (2012) QTL mapping for seedling traits in wheat grown under varying concentrations of N, P and K nutrients. Theor Appl Genet 124:851–865. https://doi.org/10.1007/s00122-011-1749-7

Hafsi C, Atia A, Lakhdar A, Debez A, Abdelly C (2011) Differential responses in potassium absorption and use efficiencies in the halophytes *Catapodium rigidum* and *Hordeum maritimum* to various potassium concentrations in the medium. Plant Prod Sci 14:135–140

Hammond JP, Broadley MR, White PJ, King GJ, Bowen HC, Hayden R, Meacham MC, Mead A, Overs T, Spracklen WP, Greenwood DJ (2009) Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architecture traits. J Exp Bot 60:1953–1968. https://doi.org/10.1093/jxb/erp083

Harada H, Leigh RA (2006) Genetic mapping of natural variation in potassium concentrations in shoots of *Arabidopsis thaliana*. J Exp Bot 57:953–960. https://doi.org/10.1093/jxb/erj081

Henry A, Doucette W, Norton J, Bugbee B (2007) Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. J Environ Qual 36:904–912. https://doi.org/10.2134/jeq2006.0425sc

Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci 11:610–617. https://doi.org/10.1016/j.tplants.2006.10.007

Hinsinger P (1998) How do plant roots acquire mineral nutrients? Chemical processes involved in the rhizosphere. Adv Agron 64:225–265. https://doi.org/10.1016/S0065-2113(08)60506-4

Hinsinger P (2013) Plant-induced changes of soil processes and properties. In: Gregory PJ, Nortcliff S (eds) Soil conditions and plant growth. Blackwell, Oxford, pp 323–365. https://doi.org/10.1002/9781118337295.ch10

Hinsinger P, Bell M, White PJ (2017) Root traits and rhizosphere characteristics determining potassium acquisition from soils. In: Murrell TS, Mikkelsen RL (eds) Proceedings for the frontiers of potassium science conference, Rome, Italy, 25–27. January 2017. International Plant Nutrition Institute, Peachtree Corners, GA, USA, pp 289–299. https://www.apni.net/kfrontiers/. Accessed 28 Sept 2020

Hocking PJ, Pate JS (1977) Mobilization of minerals to developing seeds of legumes. Ann Bot 41:1259–1278. https://doi.org/10.1093/oxfordjournals.aob.a085415

Høgh-Jensen H, Pedersen MB (2003) Morphological plasticity by crop plants and their potassium use efficiency. J Plant Nutr 26:969–984. https://doi.org/10.1081/PLN-120020069

Hoveland CS, Buchanan GA, Harris MC (1976) Response of weeds to soil phosphorus and potassium. Weed Sci 24:194–201. https://doi.org/10.1017/S0043174500065747

Jia Y-B, Yang X-E, Feng Y, Jilani G (2008) Differential response of root morphology to potassium deficient stress among rice genotypes varying in potassium efficiency. J Zhejiang Univ Sci B 9:427–434. https://doi.org/10.1631/jzus.B0710636

Johnson CR (1973) Symptomatology and analyses of nutrient deficiencies produced on flowering annual plants. Commun Soil Sci Plant Anal 4:185–196. https://doi.org/10.1080/00103627309366436

Jungk A (2001) Root hairs and the acquisition of plant nutrients from soil. J Plant Nutr Soil Sci 164:121–129. https://doi.org/10.1002/1522-2624(200104)164:2<121::AID-JPLN121>3.0.CO;2-6

Jungk A, Claassen N (1997) Ion diffusion in the soil-root system. Adv Agron 61:53–110. https://doi.org/10.1016/S0065-2113(08)60662-8

Kanter U, Hauser A, Michalke B, Draexl S, Schaeffner AR (2010) Caesium and strontium accumulation in shoots of *Arabidopsis thaliana*: genetic and physiological aspects. J Exp Bot 61:3995–4009. https://doi.org/10.1093/jxb/erq213

Khan MSK, Saeed M, Iqbal J (2015) Identification of quantitative trait loci for Na^+, K^+ and Ca^{++} accumulation traits in rice grown under saline conditions using F_2 mapping population. J Braz Bot 38:555–565. https://doi.org/10.1007/s40415-015-0160-z

Kong F-M, Guo Y, Liang X, Wu C-H, Wang Y-Y, Zhao Y, Li S-S (2013) Potassium (K) effects and QTL mapping for K efficiency traits at seedling and adult stages in wheat. Plant Soil 373:877–892. https://doi.org/10.1007/s11104-013-1844-4

Koyama ML, Levesley A, Koebner RMD, Flowers TJ, Yeo AR (2001) Quantitative trait loci for component physiological traits determining salt tolerance in rice. Plant Physiol 125:406–422. https://doi.org/10.1104/pp.125.1.406

Kuchenbuch RO, Buczko U (2011) Re-visiting potassium- and phosphate-fertilizer responses in field experiments and soil-test interpretations by means of data mining. J Plant Nutr Soil Sci 174:171–185. https://doi.org/10.1002/jpln.200900162

Kuhlmann H (1990) Importance of the subsoil for the K-nutrition of crops. Plant Soil 127:129–136. https://doi.org/10.1007/BF00010845

Kuijken RCP, van Eeuwijk FA, Marcelis LFM, Bouwmeester HJ (2015) Root phenotyping: from component trait in the lab to breeding. J Exp Bot 66:5389–5401. https://doi.org/10.1093/jxb/erv239

Kuzmanova L, Kostadinova S, Ganusheva N (2014) Efficiency of potassium in barley genotypes. Turk J Agric Nat Sci S1:584–589

Li HY, Si DX, Lv FT (2015) Differential responses of six Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*) cultivars to potassium ion deficiency. J Hortic Sci Biotechnol 90:483–488

Lin HX, Zhu MZ, Yano M, Gao JP, Liang ZW, Su WA, Hu XH, Ren ZH, Chao DY (2004) QTLs for Na^+ and K^+ uptake of the shoots and roots controlling rice salt tolerance. Theor Appl Genet 108:253–260. https://doi.org/10.1007/s00122-003-1421-y

Liu G, Li Y, Porterfield DM (2009) Genotypic differences in potassium nutrition in lowland rice hybrids. Commun Soil Sci Plant Anal 40:1803–1821. https://doi.org/10.1080/00103620902896704

Liu S, Lacape J-M, Constable GA, Llewellyn DJ (2015) Inheritance and QTL mapping of leaf nutrient concentration in a cotton inter-specific derived RIL population. PLoS One 10(5): e0128100. https://doi.org/10.1371/journal.pone.0128100

Liu H, White PJ, Li C (2016) Biomass partitioning and rhizosphere responses of maize and faba bean to phosphorus deficiency. Crop Pasture Sci 67:847–856. https://doi.org/10.1071/CP16015

Lu ZF, Lu JW, Pan YH, Li XK, Cong RH, Ren T (2016) Genotypic variation in photosynthetic limitation responses to K deficiency of *Brassica napus* is associated with potassium utilisation efficiency. Funct Plant Biol 43:880–891. https://doi.org/10.1071/FP16098

Lynch JP (2007) Roots of the second green revolution. Aust J Bot 55:493–512. https://doi.org/10.1071/BT06118

Lynch JP (2015) Root phenes that reduce the metabolic costs of soil exploration: opportunities for 21st century agriculture. Plant Cell Environ 38:1775–1784. https://doi.org/10.1111/pce.12451

Maeght J-L, Rewald B, Pierret A (2013) How to study deep roots – and why it matters. Front Plant Sci 4:299. https://doi.org/10.3389/fpls.2013.00299

Maillard A, Diquélou S, Billard V, Laîné P, Garnica M, Prudent M, Garcia-Mina J-M, Yvin J-C, Ourry A (2015) Leaf mineral nutrient remobilization during leaf senescence and modulation by nutrient deficiency. Front Plant Sci 6:317. https://doi.org/10.3389/fpls.2015.00317

Marchi G, Silva VA, Guilherme LRG, Lima JM, Nogueira FD, Guimaraes PTG (2012) Potassium extractability from soils of Brazilian coffee regions. Biosci J 28:913–919

Memon AR, Saccomani M, Glass ADM (1985) Efficiency of potassium utilization by barley varieties: the role of subcellular compartmentation. J Exp Bot 36:1860–1876. https://doi.org/10.1093/jxb/36.12.1860

Mengel K, Kirkby EA, Kosegarten H, Appel T (2001) Principles of plant nutrition. Kluwer Academic, Dordrecht

Milla R, Castro-Díez P, Maestro-Martínez M, Montserrat-Martí G (2005) Relationships between phenology and the remobilization of nitrogen, phosphorus and potassium in branches of eight Mediterranean evergreens. New Phytol 168:167–178. https://doi.org/10.1111/j.1469-8137.2005.01477.x

Minjian C, Haiqiu Y, Hongkui Y, Chunji J (2007) Difference in tolerance to potassium deficiency between two maize inbred lines. Plant Prod Sci 10:42–46. https://doi.org/10.1626/pps.10.42

Miyamoto T, Ochiai K, Takeshita S, Matoh T (2012) Identification of quantitative trait loci associated with shoot sodium accumulation under low potassium conditions in rice plants. Soil Sci Plant Nutr 58:728–736. https://doi.org/10.1080/00380768.2012.745797

Moreira A, Moraes LAC, Fageria NK (2015) Variability on yield, nutritional status, soil fertility, and potassium-use efficiency by soybean cultivar in acidic soil. Commun Soil Sci Plant Anal 46:2490–2508. https://doi.org/10.1080/00103624.2015.1085555

Moriconi JI, Santa-María GE (2013) A theoretical framework to study potassium utilization efficiency in response to withdrawal of potassium. J Exp Bot 64:4289–4299. https://doi.org/10.1093/jxb/ert236

Moriconi JI, Buet A, Simontacchi M, Santa-María GE (2012) Near-isogenic wheat lines carrying altered function alleles of the *Rht-1* genes exhibit differential responses to potassium deprivation. Plant Sci 185/186:199–207. https://doi.org/10.1016/j.plantsci.2011.10.011

Munns R, James RA, Xu B, Athman A, Conn SJ, Jordans C, Byrt CS, Hare RA, Tyerman SD, Tester M, Plett D, Gilliham M (2012) Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. Nat Biotechnol 30:360–364. https://doi.org/10.1038/nbt.2120

Nawaz I, Zia-ul-hassan, Ranjha AM, Arshad M (2006) Exploiting genotypic variation among fifteen maize genotypes of Pakistan for potassium uptake and use efficiency in solution culture. Pak J Bot 38:1689–1696

Neumann G, Römheld V (2012) Rhizosphere chemistry in relation to plant nutrition. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic, London, pp 347–368. https://doi.org/10.1016/B978-0-12-384905-2.00014-5

Nguyen VL, Dolstra O, Malosetti M, Kilian B, Graner A, Visser RGF, van der Linden CG (2013a) Association mapping of salt tolerance in barley (*Hordeum vulgare* L.). Theor Appl Genet 126:2335–2351. https://doi.org/10.1007/s00122-013-2139-0

Nguyen VL, Ribot SA, Dolstra O, Niks RE, Visser RGF, van der Linden CG (2013b) Identification of quantitative trait loci for ion homeostasis and salt tolerance in barley (*Hordeum vulgare* L). Mol Breed 31:137–152. https://doi.org/10.1007/s11032-012-9777-9

Nieves-Cordones M, Martinez V, Benito B, Rubio F (2016) Comparison between arabidopsis and rice for main pathways of K^+ and Na^+ uptake by roots. Front Plant Sci 7:992. https://doi.org/10.3389/fpls.2016.00992

Ning P, Li S, Yu P, Zhang Y, Li C (2013) Post-silking accumulation and partitioning of dry matter, nitrogen, phosphorus and potassium in maize varieties differing in leaf longevity. Field Crops Res 144:19–27. https://doi.org/10.1016/j.fcr.2013.01.020

Pettersson S, Jensén P (1983) Variation among species and varieties in uptake and utilization of potassium. Plant Soil 72:231–237. https://doi.org/10.1007/BF02181962

Pretty KM, Stangel PJ (1985) Current and future use of world potassium. In: Munson RD (ed) Potassium in agriculture. ASA, CSSA & SSSA, Madison, pp 99–128

Prinzenberg AE, Barbier H, Salt DE, Stich B, Matthieu R (2010) Relationships between growth, growth response to nutrient supply, and ion content using a recombinant inbred line population in Arabidopsis. Plant Physiol 154:1361–1371. https://doi.org/10.1104/pp.110.161398

Qi Z, Hampton CR, Shin R, Barkla BJ, White PJ, Schachtman DP (2008) The high affinity K^+ transporter AtHAK5 plays a physiological role *in planta* at very low K^+ concentrations and provides a caesium uptake pathway in Arabidopsis. J Exp Bot 59:595–607. https://doi.org/10.1093/jxb/erm330

Ren H-Z, Goa J-P, Li L-G, Cai X-L, Huang W, Chao D-Y, Zhu M-Z, Wang Z-Y, Luan S, Lin H-X (2005) A rice quantitative trait locus for salt tolerance encodes a sodium transporter. Nat Genet 37:1141–1146. https://doi.org/10.1038/ng1643

Rengel Z, Damon PM (2008) Crops and genotypes differ in efficiency of potassium uptake and use. Physiol Plant 133:624–636. https://doi.org/10.1111/j.1399-3054.2008.01079.x

Rengel Z, Djalovic I (2017) Differential potassium-use efficiency in crops and genotypes. In: Murrell TS, Mikkelsen RL (eds) Proceedings for the frontiers of potassium science conference, 25–27 January 2017, Rome, Italy. International Plant Nutrition Institute, Peachtree Corners, pp 65–73. https://www.apni.net/k-frontiers/. Accessed 29 May 2020

Rengel Z, Marschner P (2005) Nutrient availability and management in the rhizosphere: exploiting genotypic differences. New Phytol 168:305–312. https://doi.org/10.1111/j.1469-8137.2005.01558.x

Rochester IJ, Constable GA (2015) Improvements in nutrient uptake and nutrient use-efficiency in cotton cultivars released between 1973 and 2006. Field Crops Res 173:14–21. https://doi.org/10.1016/j.fcr.2015.01.001

Römheld V (2012) Diagnosis of deficiency and toxicity of nutrients. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic, London, pp 299–312. https://doi.org/10.1016/B978-0-12-384905-2.00011-X

Römheld V, Kirkby EA (2010) Research on potassium in agriculture: needs and prospects. Plant Soil 335:155–180. https://doi.org/10.1007/s11104-010-0520-1

Rose TJ, Rengel Z, Ma Q, Bowden JW (2007) Differential accumulation patterns of phosphorus and potassium by canola cultivars compared to wheat. J Plant Nutr Soil Sci 170:404–411. https://doi.org/10.1002/jpln.200625163

Ryan PR, Tyerman SD, Sasaki T, Furuichi T, Yamamoto Y, Zhang WH, Delhaize E (2011) The identification of aluminium-resistance genes provides opportunities for enhancing crop production on acid soils. J Exp Bot 62:9–20. https://doi.org/10.1093/jxb/erq272

Samal D, Kovar JL, Steingrobe B, Sadana US, Bhadoria PS, Claassen N (2010) Potassium uptake efficiency and dynamics in the rhizosphere of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), and sugar beet (*Beta vulgaris* L.) evaluated with a mechanistic model. Plant Soil 332:105–121. https://doi.org/10.1007/s11104-009-0277-6

Sánchez-Rodríguez E, del Mar Rubio-Wilhelmi M, Cervilla LM, Blasco B, Rios JJ, Leyva R, Romero L, Ruiz JM (2010) Study of the ionome and uptake fluxes in cherry tomato plants under moderate water stress conditions. Plant Soil 335:339–347. https://doi.org/10.1007/s11104-010-0422-2

Sanes FSM, Castilhos RMV, Scivittaro WB, Vahl LC, de Morais JR (2013) Root morphology and potassium uptake kinetic parameters in irrigated rice genotypes. Rev Bras Ciênc Solo 37:688–697. https://doi.org/10.1590/S0100-06832013000300015

Santa-María GE, Moriconi JI, Oliferuk S (2015) Internal efficiency of nutrient utilization: what is it and how to measure it during vegetative plant growth? J Exp Bot 66:3011–3018. https://doi.org/10.1093/jxb/erv162

Schilling G, Eißner H, Schmidt L, Peiter E (2016) Yield formation of five crop species under water shortage and differential potassium supply. J Plant Nutr Soil Sci 179:234–243. https://doi.org/10.1002/jpln.201500407

Shi W, Wang X, Yan W (2004) Distribution patterns of available P and K in rape rhizosphere in relation to genotypic difference. Plant Soil 261:11–16. https://doi.org/10.1023/B:PLSO.0000035571.26352.99

Siddiqi MY, Glass ADM (1983a) Studies of the growth and mineral nutrition of barley varieties. I. Effect of potassium supply on the uptake of potassium and growth. Can J Bot 61:671–678. https://doi.org/10.1139/b83-076

Siddiqi MY, Glass ADM (1983b) Studies of the growth and mineral nutrition of barley varieties. II. Potassium uptake and its regulation. Can J Bot 61:1551–1558. https://doi.org/10.1139/b83-167

Siddiqi MY, Glass ADM, Hsiao AI, Minjas AN (1987) Genetic differences among wild oat lines in potassium uptake and growth in relation to potassium supply. Plant Soil 99:93–105. https://doi.org/10.1007/BF02370157

Spear SN, Asher CJ, Edwards DG (1978a) Response of cassava, sunflower, and maize to potassium concentration in solution. I. Growth and plant potassium concentration. Field Crops Res 1:347–361. https://doi.org/10.1016/0378-4290(78)90036-9

Spear SN, Asher CJ, Edwards DG (1978b) Response of cassava, sunflower, and maize to potassium concentration in solution. II. Potassium absorption and its relation to growth. Field Crops Res 1:363–373. https://doi.org/10.1016/0378-4290(78)90037-0

Steingrobe B, Claassen N (2000) Potassium dynamics in the rhizosphere and K efficiency of crops. J Plant Nutr Soil Sci 163:101–106. https://doi.org/10.1002/(SICI)1522-2624(200002)163:1<101::AID-JPLN101>3.0.CO;2-J

Stelling D, Wang S-H, Römer W (1996) Efficiency in the use of phosphorus, nitrogen and potassium in *topless* faba beans (*Vicia faba* L.) – variability and inheritance. Plant Breed 115:361–366. https://doi.org/10.1111/j.1439-0523.1996.tb00934.x

Tao Y, Wang L, Wang X, Xia Y, Wan K, Chen F (2012) Adaptive phenotypic differences to low potassium soil of two cotton genotypes with various potassium-use efficiencies. Commun Soil Sci Plant Anal 43:1984–1993. https://doi.org/10.1080/00103624.2012.693230

Thomas CL, Graham NS, Hayden R, Meacham MC, Neugebauer K, Nightingale M, Dupuy LX, Hammond JP, White PJ, Broadley MR (2016) High-throughput phenotyping (HTP) identifies seedling root traits linked to variation in seed yield and nutrient capture in field-grown oilseed rape (*Brassica napus* L.). Ann Bot 118:655–665. https://doi.org/10.1093/aob/mcw046

Thorup-Kristensen K, Halberg N, Nicolaisen M, Olesen JE, Crews TE, Hinsinger P, Kirkegaard J, Pierret A, Dresbøll DB (2020) Digging deeper for agricultural resources, the value of deep rooting. Trends Plant Sci 25:406–417. https://doi.org/10.1016/j.tplants.2019.12.007

Trehan SP (2005) Nutrient management by exploiting genetic diversity of potato – a review. Potato J 32:1–15

Trehan SP, Singh BP (2013) Nutrient efficiency of different crop species and potato varieties – in retrospect and prospect. Potato J 40:1–21

Végh KR, Köszegi B, Gupta SC (2008) Bioavailability of soil potassium for different crops. Cereal Res Commun 36:1883–1886

Véry AA, Nieves-Cordones M, Daly M, Khan I, Fizames C, Sentenac H (2014) Molecular biology of K^+ transport across the plant cell membrane: what do we learn from comparison between plant species? J Plant Physiol 171:748–769. https://doi.org/10.1016/j.jplph.2014.01.011

Villalta I, Reina-Sánchez A, Bolarín MC, Cuartero J, Belver A, Venema K, Carbonell EA, Asins MJ (2008) Genetic analysis of Na^+ and K^+ concentrations in leaf and stem as physiological components of salt tolerance in tomato. Theor Appl Genet 116:869–880. https://doi.org/10.1007/s00122-008-0720-8

Wakeel A, Farooq M, Qadir M, Schubert S (2011) Potassium substitution by sodium in plants. Crit Rev Plant Sci 30:401–413. https://doi.org/10.1080/07352689.2011.587728

Wang JG, Zhang FS, Cao YP, Zhang XL (2000) Effect of plant types on release of mineral potassium from gneiss. Nutr Cycl Agroecosyst 56:37–44. https://doi.org/10.1023/A:1009826111929

Wang H-Y, Shen Q-H, Zhou J-M, Wang J, Du C-W, Chen X-Q (2011) Plants use alternative strategies to utilize nonexchangeable potassium in minerals. Plant Soil 343:209–220. https://doi.org/10.1007/s11104-011-0726-x

Wang Z, Chen Z, Cheng J, Lai Y, Wang J, Bao Y, Huang J, Zhang H (2012) QTL analysis of Na^+ and K^+ concentrations in roots and shoots under different levels of NaCl stress in rice (*Oryza sativa* L.). PLoS One 7(12):e51202. https://doi.org/10.1371/journal.pone.0051202

Wang JD, Wang H, Zhang Y, Zhou J, Chen X (2015a) Intraspecific variation in potassium uptake and utilization among sweet potato (*Ipomoea batatas* L.) genotypes. Field Crops Res 170:76–82. https://doi.org/10.1016/j.fcr.2014.10.007

Wang X-G, Zhao X-H, Jiang C-J, Li C-H, Cong S, Wu D, Chen Y-Q, Yu H-Q, Wang C-Y (2015b) Effects of potassium deficiency on photosynthesis and photoprotection mechanisms in soybean (*Glycine max* (L.) Merr.). J Integr Agric 14:856–863. https://doi.org/10.1016/S2095-3119(14)60848-0

Watanabe T, Broadley MR, Jansen S, White PJ, Takada J, Satake K, Takamatsu T, Tuah SJ, Osaki M (2007) Evolutionary control of leaf element composition in plants. New Phytol 174:516–523. https://doi.org/10.1111/j.1469-8137.2007.02078.x

White PJ (1993) Relationship between the development and growth of rye (*Secale cereale* L.) and the potassium concentration in solution. Ann Bot 72:349–358. https://doi.org/10.1006/anbo.1993.1118

White PJ (2013) Improving potassium acquisition and utilisation by crop plants. J Plant Nutr Soil Sci 176:305–316. https://doi.org/10.1002/jpln.201200121

White PJ (2016) Biofortification of edible crops. In: eLS. Wiley, Chichester. https://doi.org/10.1002/9780470015902.a0023743

White PJ (2020) Potassium in crop physiology. In: Rengel Z (ed) Achieving sustainable crop nutrition. Burleigh Dodds, Cambridge, pp 213–236. https://doi.org/10.19103/AS.2019.0062.10

White PJ, Bell MJ (2017) The genetics of potassium uptake and utilization in plants. In: Murrell TS, Mikkelsen RL (eds) Proceedings for the frontiers of potassium science conference, 25–-27 January 2017, Rome. International Plant Nutrition Institute, Peachtree Corners, pp 46–65. https://www.apni.net/k-frontiers/. Accessed 29 May 2020

White PJ, Greenwood DJ (2013) Properties and management of cationic elements for crop growth. In: Gregory PJ, Nortcliff S (eds) Soil conditions and plant growth. Blackwell, Oxford, pp 160–194. https://doi.org/10.1002/9781118337295.ch6

White PJ, Karley AJ (2010) Potassium. In: Hell R, Mendel R-R (eds) Cell biology of metals and nutrients. Springer, Berlin, pp 199–224. https://doi.org/10.1007/978-3-642-10613-2_9

White PJ, Broadley MR, Greenwood DJ, Hammond JP (2005) Genetic modifications to improve phosphorus acquisition by roots. In: Proceedings of the International Fertiliser Society 568. IFS, York. ISBN: 0853102058

White PJ, Bradshaw JE, Dale MFB, Ramsay G, Hammond JP, Broadley MR (2009) Relationships between yield and mineral concentrations in potato tubers. HortScience 44:6–11. https://doi.org/10.21273/HORTSCI.44.1.6

White PJ, Hammond JP, King GJ, Bowen HC, Hayden RM, Meacham MC, Spracklen WP, Broadley MR (2010) Genetic analysis of potassium use efficiency in *Brassica oleracea*. Ann Bot 105:1199–1210. https://doi.org/10.1093/aob/mcp253

White PJ, Broadley MR, Thompson JA, McNicol JW, Crawley MJ, Poulton PR, Johnston AE (2012) Testing the distinctness of shoot ionomes of angiosperm families using the Rothamsted Park Grass Continuous Hay experiment. New Phytol 196:101–109. https://doi.org/10.1111/j.1469-8137.2012.04228.x

White PJ, George TS, Gregory PJ, Bengough AG, Hallett PD, McKenzie BM (2013) Matching roots to their environment. Ann Bot 112:207–222. https://doi.org/10.1093/aob/mct123

White PJ, Kawachi T, Thompson JA, Wright G, Dupuy LX (2016) Minimising the treatments required to determine the responses of different crop genotypes to potassium supply. Commun Soil Sci Plant Anal 47.(S1:104–111. https://doi.org/10.1080/00103624.2016.1232103

White PJ, Bowen HC, Broadley MR, El-Serehy HA, Neugebauer K, Taylor A, Thompson JA, Wright G (2017) Evolutionary origins of abnormally large shoot sodium accumulation in non-saline environments within the Caryophyllales. New Phytol 214:284–293. https://doi.org/10.1111/nph.14370

Wild A, Skarlou V, Clement CR, Snaydon RW (1974) Comparison of potassium uptake by four plant species grown in sand and in flowing solution culture. J Appl Ecol 11:801–812

Wishart J, George TS, Brown LK, Ramsay G, Bradshaw JE, White PJ, Gregory PJ (2013) Measuring variation in potato roots in both field and glasshouse: the search for useful yield predictors and a simple screen for root traits. Plant Soil 368:231–249. https://doi.org/10.1007/s11104-012-1483-1

Woodend JJ, Glass ADM (1993) Genotype-environment interaction and correlation between vegetative and grain production measures of potassium use-efficiency in wheat (*T. aestivum* L.) grown under potassium stress. Plant Soil 151:39–44. https://doi.org/10.1007/BF00010784

Wu P, Ni JJ, Luo AC (1998) QTLs underlying rice tolerance to low-potassium stress in rice seedlings. Crop Sci 38:1458–1462

Wu J, Yuan Y-X, Zhang X-W, Zhao J, Song X, Li Y, Li X, Sun R, Koornneef M, Aarts MGM, Wang X-W (2008) Mapping QTLs for mineral accumulation and shoot dry biomass under different Zn nutritional conditions in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*). Plant Soil 310:25–40. https://doi.org/10.1007/s11104-008-9625-1

Wu J-T, Zhang X-Z, Li T-X, Yu H-Y, Huang P (2011) Differences in the efficiency of potassium (K) uptake and use in barley varieties. Agric Sci China 10:101–108. https://doi.org/10.1016/S1671-2927(11)60312-X

Yang XE, Liu JX, Wang WM, Li H, Luo AC, Ye ZQ, Yang Y (2003) Genotypic differences and some associated plant traits in potassium internal use efficiency of lowland rice (*Oryza sativa* L.). Nutr Cycl Agroecosyst 67:273–282. https://doi.org/10.1023/B:FRES.0000003665.90952.0c

Yang XE, Liu JX, Wang WM, Ye ZQ, Luo AC (2004) Potassium internal use efficiency relative to growth vigor, potassium distribution, and carbohydrate allocation in rice genotypes. J Plant Nutr 27:837–852. https://doi.org/10.1081/PLN-120030674

Yang F, Wang G, Zhang Z, Eneji AE, Duan L, Li Z, Tian X (2011) Genotypic variations in potassium uptake and utilization in cotton. J Plant Nutr 34:83–97. https://doi.org/10.1080/01904167.2011.531361

Yu P, Li X, White PJ, Li C (2015) A large and deep root system underlies high nitrogen-use efficiency in maize production. PLoS One 10(5):e0126293. https://doi.org/10.1371/journal.pone.0126293

Zdunić Z, Grljušić S, Ledenčan T, Duvnjak T, Šimić D (2014) Quantitative trait loci mapping of metal concentrations in leaves of the maize IBM population. Hereditas 151:55–60. https://doi.org/10.1111/hrd2.00048

Zhang G, Chen J, Tirore EA (1999) Genotypic variation for potassium uptake and utilization efficiency in wheat. Nutr Cycl Agroecosyst 54:41–48. https://doi.org/10.1023/A:1009708012381

Zhang Z, Tian X, Duan L, Wang B, He Z, Li Z (2007) Differential responses of conventional and Bt-transgenic cotton to potassium deficiency. J Plant Nutr 30:659–670. https://doi.org/10.1080/01904160701289206

Zhang Y, Zhang C-C, Yan P, Chen X-P, Yang J-C, Zhang F-S, Cui Z-L (2013) Potassium requirement in relation to grain yield and genotypic improvement of irrigated lowland rice in China. J Plant Nutr Soil Sci 176:400–406. https://doi.org/10.1002/jpln.201200206

Zhao Y, Li X-Y, Zhang S-H, Wang J, Yang X-F, Tian J-C, Hai Y, Yang X-J (2014) Mapping QTLs for potassium-deficiency tolerance at the seedling stage in wheat (*Triticum aestivum* L.). Euphytica 198:185–198. https://doi.org/10.1007/s10681-014-1091-7

Zia-ul-hassan, Arshad M (2011) Relationship among root characteristics and differential potassium uptake and use efficiency of selected cotton genotypes under potassium deficiency. Pak J Bot 43:1831–1835

Zia-ul-hassan, Kubar KA, Rajpar I, Shah AN, Tunio SD, Shah JA, Maitlo AA (2014) Evaluating potassium-use-efficiency of five cotton genotypes of Pakistan. Pak J Bot 46:1237–1242

Zörb C, Senbayram M, Peiter E (2014) Potassium in agriculture – status and perspectives. J Plant Physiol 171:656–669. https://doi.org/10.1016/j.jplph.2013.08.008