

T. Scott Murrell · Robert L. Mikkelsen
Gavin Sulewski · Robert Norton
Michael L. Thompson *Editors*

Improving Potassium Recommendations for Agricultural Crops

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Dedication

This book is dedicated to the scientists, staff, and supporters of the International Plant Nutrition Institute (2007–2019), its predecessor, the Potash & Phosphate Institute (1977–2006), and its predecessor, the Potash Institute (1935–1977). At the initial founding of the Potash Institute in 1935 in Washington, DC, Dr. J.W. Turrentine, the first president, spoke to the Institute's first Board, comprising eight members from the potash companies of that time:

Agricultural usage of potash must be increased on a basis that is sound and profitable to the farmer. Consumer betterment is basic. . . If we did not believe that, we should have no moral justification as an Institute. Since that time, the scientists working for the Institute have striven to be objective, gathering evidence to determine when fertilizer was the best option to improve crop productivity and farmer profitability, and when it was not. Over the decades, the Institute became global in scope, creating positive impacts in most countries around the

world—a remarkable feat considering the few scientists ever employed. The compass stayed true over those decades, exemplified by the mission of the International Plant Nutrition Institute, “to develop and promote scientific information about the responsible management of plant nutrition for the benefit of the human family.” The newly formed African Plant Nutrition Institute, the phoenix organization, keeps the needle true with its mission to “innovate plant nutrition through evidence-based practices for a resilient and food secure Africa.”

The Institute in its various rebirths has always been a unique organization, with highly respected scientists passionate about feeding hungry people and improving the livelihoods of farmers. There will always be a need to take the most compelling scientific evidence and apply it effectively to everyday practical problems. This book is but one of thousands of examples of the Institute’s passion for bringing together diverse ideas to find new solutions. As a reader, we invite you to share in that passion and carry it forward.

Foreword

The publication of *Improving Potassium Recommendations for Agricultural Crops* is occurring 35 years after the last major scientific book on potassium (K) in agriculture. The previous book, published by the American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, was over 1200 pages in length and offered a comprehensive global review of the topics ranging from world K reserves and mining to K nutrition for specific crops and everything in between. It was truly global in subject matter, geography, and authorship. Like the earlier book, this book is global in geography and authorship, but is more narrowly focused on the science supporting K recommendations for agronomic crops and their improvement. So, why the focus on recommendations and why is there an urgent need for such a book?

As one of the three primary plant nutrients, K remains critically important in crop production. As an essential element for human nutrition, K intake today is inadequate in the diets of most of the world's population. The need for improved cropping system productivity and the need for efficient use of all local resources and external inputs, including K and inputs with which K interacts, have greatly elevated the need to predict the capacity of specific soils to meet the K needs of specific crops. When that capacity is found insufficient, effective guidelines for K source, rate, timing, and placement decisions are needed. In the past few decades, the adoption of both high-tech and low-tech approaches to site-specific nutrient management has increased the demand for accuracy and precision in K recommendations. Soil K evaluation has increased in importance in regions of the world where long-term negative K balances have increased the frequency of K deficiency in crops. In many areas, desired accuracy and precision are not attainable with current K recommendation approaches.

At the same time, substantial growth has occurred in basic knowledge of the mechanisms of K cycling in soils, the function of K in plants and animals, and how growing plants and healthy soils interact. Much of this growth is highly relevant to the K recommendation process. However, this new scientific understanding and underlying data have not undergone the same degree of synthesis experienced with

nitrogen (N) or phosphorus (P). Therefore, it is not readily accessible to those responsible for recommendations or to growers and their advisers.

A special challenge in drawing attention to the need for increased emphasis on the science and practice of K management is the insidious nature of most K deficiencies. With N, serious management problems are often catastrophic where it becomes obvious that the crop is suffering and requires attention. In extreme cases, K deficiency can also be catastrophic where clear deficiency symptoms appear along with stunted growth. However, K deficiencies are often less pronounced, without clear symptoms, causing such problems to go undetected and providing less incentive for a change in practices to address the cause of the problem—termed “hidden hunger” in past literature.

This book is part of a process initiated by the International Plant Nutrition Institute to enable the integration of new knowledge of K into K recommendations and management. The process began in 2013 with informal workshops held in the USA and in Turkey designed to gather input from scientists on the major issues of K plant nutrition. These were followed in 2015 by the Frontiers in Potassium Science Workshop held in Hawaii in conjunction with the International Symposium on Soil and Plant Analysis. That workshop succeeded in creating a global network of innovative scientists who effectively communicate across disciplines to advance the science of soil and plant K evaluation and to further communicate those advances to applied scientists and to the private sector. One outcome of the workshop was a roadmap to guide future efforts to advance the science of soil K evaluation. That roadmap was instrumental in planning “Frontiers of Potassium—an International Conference” held in January of 2017 in Rome, Italy. The papers presented at the 3-day Rome conference became the core of this book.

But why a book . . . and why now? This book advocates for a paradigm shift in K recommendations. In his 1992 book, *Future Edge*, Joel Barker described what causes a paradigm to shift. He stated that every paradigm develops a special set of problems that everyone in the field wants to be able to solve but no one knows how to do it. These problems are “put on the shelf” with a promise made that we will get back to them sooner or later. When the weight of these special problems approaches a critical mass, the paradigm shifts. We believe current K recommendations are at that point.

Problems of K that are currently “on the shelf” and that motivated development of this book include but are not limited to the following.

- Lack of definitive calibration of soil test K to crop response in some areas
- Within a given soil test range, great variability in response to applied K among growing seasons at a single site, or among sites within a single growing season
- All too frequent lack of responses to K applications on soils testing low in exchangeable K levels
- All too frequent responses to K applications on soils where none were expected, based on high or very high levels of exchangeable K
- Unexpected spatial variability patterns of soil test K within fields

- Large temporal variability in soil test K that appears unrelated to K additions or K removal by crops and contributes to substantial “noise” in long-term soil test records
- Directionally inconsistent effects of weather-related factors, such as soil moisture content, on soil test K levels across sites in both research plots and grower fields
- Alterations in measured K levels and their interpretation due to sampling or sample handling procedures
- Genetic changes in crops that impact progressive K demand through the growing season and root development that may in turn influence requirements for soil K and its release to the soil solution
- Unknown impacts on surface soil test K interpretation, including changes in subsoil K levels as a result of long-term crop removal, crop susceptibility to moisture stress, and general K management
- Abandonment of K soil testing approaches in some parts of the world due to poor access to soil testing or limited supporting correlation, calibration, and interpretation

Resolution of many of these issues and problems with soil K assessment may well reside in answers to appropriate mechanistic questions about the behavior of K in soil–plant systems. This book focuses on those mechanisms. Much is already known about these issues, but only a portion of what is known is currently utilized in soil K assessment and the associated interpretation tools. We believe that this book will contribute significantly to improved synthesis of existing knowledge, facilitate its use in the recommendation process, and identify needed research to fill knowledge gaps.

This book is only part of the ongoing process to enable the integration of new knowledge into improved K recommendations and management. Numerous stakeholders need to be engaged in the future if real-world improvements in K management are to be realized. *Improving Potassium Recommendations for Agricultural Crops* provides a solid foundation for building collaborative efforts to advance the science and practice of K management. A partial list of critical stakeholders follows.

- **Farmers or growers:** They are of course the end user. They are often the first to identify problems with current practices and can help set priorities for research and development. To an increasing degree today, they can also be participants in generating data in the discovery process via “citizen science” approaches.
- **Research scientists:** The K science relevant to developing a framework for improved recommendations is in need of rigorous synthesis around the issues addressed in this book. This book will be a major step forward in that synthesis; however, additional reviews will be needed with expanded data sharing and evaluation of existing field and laboratory technologies. The complexities of the problems being addressed will likely require modeling approaches to be employed and will lead to identification of remaining knowledge gaps.
- **Laboratory services:** Analytical laboratories have a critical role to play in providing the soil and plant analyses required for more complete characterization of soil properties critical in defining potential K flux and K holding capacity.

Assessing these additional properties in a cost-effective and timely manner could be a challenge but will be essential for progress in K management. It may well involve additional research commitments in laboratory or field procedures, including sampling protocols and sensing technologies.

- **Data services:** Precipitation, temperature, and other climatic factors have a major influence on crop growth and K demand and also greatly impact numerous soil processes related to K flux. And, it is highly likely that the only cost-effective means of assessing some critical soil properties will be via digital soil classification maps. Services that can supply these data and likely others will have important roles to play.
- **Extension:** Extension, in both private and public sectors, will have a critical role in guiding knowledge synthesis and transfer, developing a framework and associated decision support systems or tools, and evaluating the effectiveness of those products. Extension is also needed to help build coalitions between research, laboratory, and data communities to keep all parties communicating and moving forward.
- **Fertilizer industry:** Timely, affordable access to appropriate K fertilizers is taken for granted in much of the world but can certainly be a limiting factor in some regions. It does little good if needs can be predicted but the products to meet those needs are inaccessible or if they do not work as advertised.
- **Local service providers:** Last-mile delivery and testing of technology and information via adaptive management with farmers or growers to fine-tune them to local conditions is an important step. Local service providers will need to use scientifically sound on-farm experimental protocols to generate data needed to inform management practice changes.

So, the time has come to address the items that have been sitting on the shelf for decades. With the right network of people and organizations, support can be found, and a pathway created for successful implementation of new solutions. Let us clear the shelf to make way for new items and the next needed paradigm shift in the future.

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Paul Fixen

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The editors and authors express appreciation to the African Plant Nutrition Institute (APNI) for the support that made publication of this book possible. During the turmoil that occurred between the dissolution of IPNI and the preparation of this book, APNI provided the resources necessary to allow completion of this important work.

Potassium is too frequently overlooked in African agriculture. Soil nutrient depletion continues to plague sub-Saharan African crop production due to low native fertility and inadequate fertilizer application. Negative K balances resulting from excessive nutrient extraction are clearly not sustainable. In North Africa, soil K concentrations are regularly assumed to be adequate for crop growth. However, closer examination commonly reveals positive crop responses to K inputs. Farmers across Africa often fail to add adequate fertilizer K due to the perceived high cost of fertilizer and lack of access.

APNI hopes that this publication will lead to renewed appreciation of the importance of K in African agriculture and for the entire world. The contributions from these leading scientists provide insight on how this nutrient can boost our shared goals of a sustainable and healthy global food supply.

Affirmation

Philip J. White was supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government.

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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

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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 (K_a) from the soil plus fertilizer ($\text{g } Y \text{ g}^{-1} K_a$) 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 ($\text{g } K_{\text{crop}} \text{ g}^{-1} K_a$) and (3) its K utilization efficiency (KUtE), which is defined as yield per unit crop K content ($\text{g } Y \text{ g}^{-1} K_{\text{crop}}$). These are often complemented by measurements of (4) the

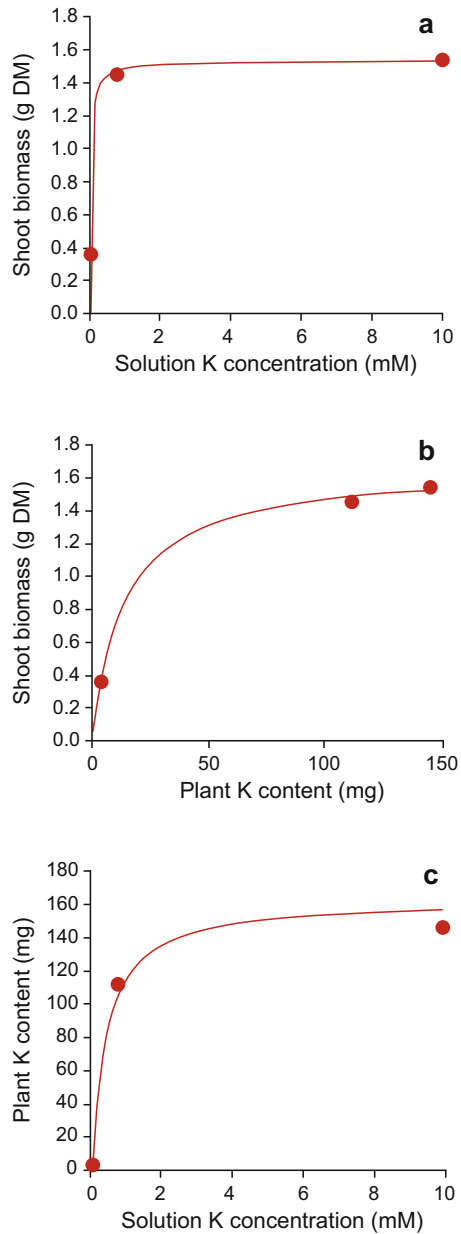
Table 5.1 Mathematical definitions of aspects of potassium (K) use efficiency in crops

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

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

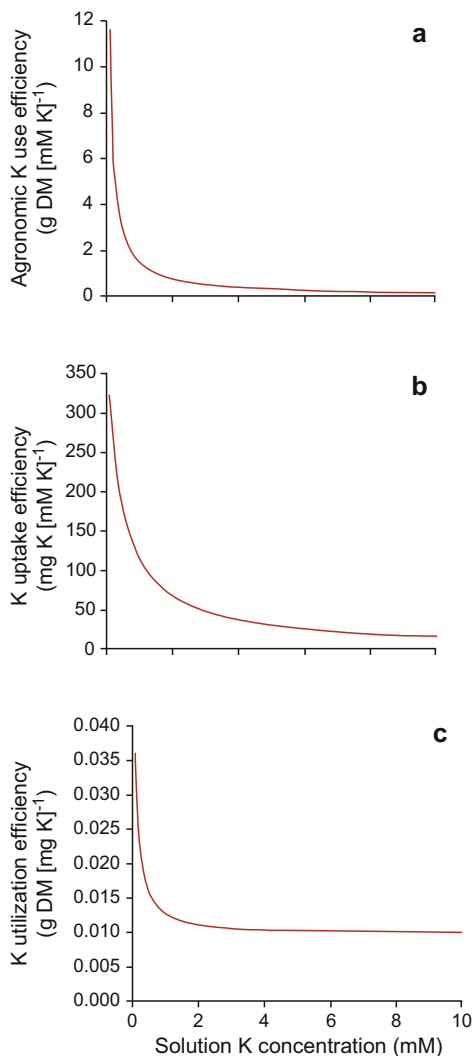
For further information see Fageria (2009), White (2013), Maillard et al. (2015) and White et al. (2016)

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 μ M, 0.75 mM, or 10 mM K^+ . Lines show regressions to the data assuming Michaelis–Menten relationships with (a) $K_{m_{Ka}} = 0.032$ mM and $Y_{max} = 1.53$ g DM, (b) $K_{m_{Kcrop}} = 13.9$ 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).

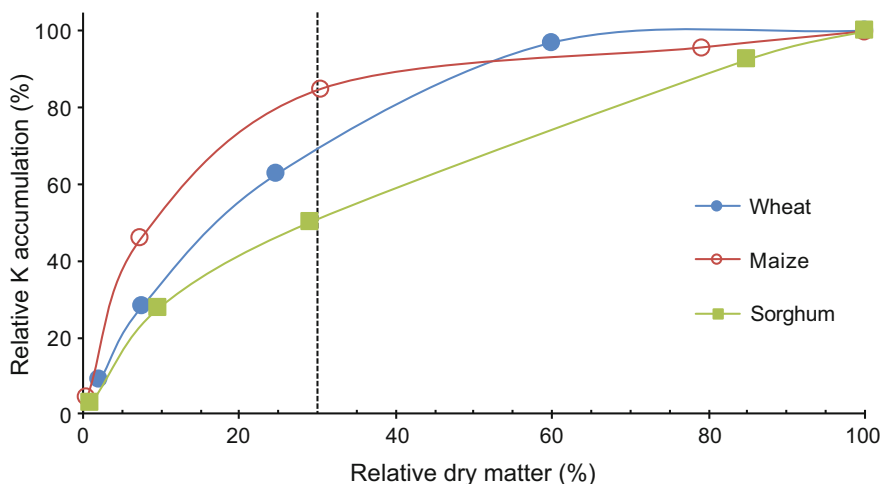


Fig. 5.3 Relative accumulation of dry matter and potassium (K) in wheat, maize, and sorghum grown to maturity in an Oxisol soil under controlled conditions in the glasshouse (Bell et al. unpublished). Maize shows the classic K accumulation curve that is well in advance of biomass in relative terms, with >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 unculm 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 ($\text{m}^2 \text{g}^{-1} \text{DM}$) 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 ($\text{mg K cm}^{-1} \text{root}$) 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 K_{utE} 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;

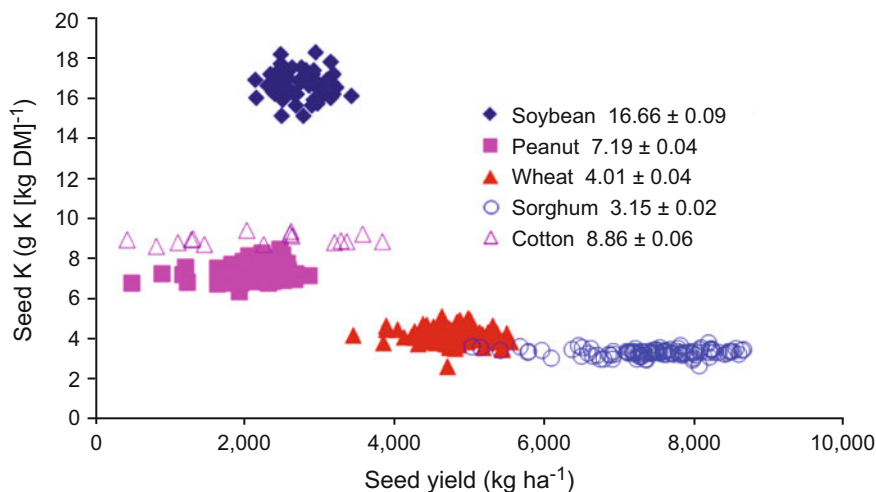


Fig. 5.4 Relationships between crop yield (as determined by variation in soil K status) and the K concentration in grains harvested from soybean, peanut, wheat, sorghum, and cotton crops grown on an Oxisol soil at Kingaroy, SE Queensland, Australia (Bell et al. unpublished). Data for each species were 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 KUE 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, KUpE, 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 SIHKT1;1 and SIHKT1;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.

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