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Potassium Efficiency of Crop Species as Related to K Dynamics in the Rhizosphere Simulated by Mathematical Modelling

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To

Ibrahim El Dessougi
and
Fathia Aburafad

from whose strength and courage
I will always draw the will to go forward

Abstract

Plant species and cultivars within a species differ greatly in their K efficiency. This study was initiated with the objective of an in-depth investigation of the possible mechanisms of K efficiency of some selected crop species.

The methodology employed in this research, was a series of pot experiments in growth chambers, at different growth conditions, a field experiment and analyses of various plant and soil parameters. It was established that the plant species studied, differ in their K efficiency as well as their efficiency mechanisms. Efficiency mechanisms established by the plant species were either a low internal K requirement or high utilisation efficiency, low nutrient demand on the roots because of a low shoot growth rate and/or a high uptake efficiency. The latter is reflected in the root morphological characteristics, for example, a large root system, root hairs or high root physiological activity expressed as a high uptake rate per unit root and time or influx.

The research hinted to possible K mobilisation by the roots of some species and to physiological adaptability to low K concentrations in the soil solution with plant age. For better understanding of the underlying mechanisms of nutrient uptake by the different plant species, K transport in soil and uptake by plants was simulated by a mechanistic model, which encompasses uptake by root hairs as well. The results revealed that under K sufficiency, the model described correctly the processes involved in K uptake from the soil. Under K deficiency, the model either over-predicted or under-predicted the actual uptake. The over-prediction was because of a wrong estimation of the uptake kinetics, and the under-prediction was because some vital processes which take place in the rhizosphere and enhance the K soil solution concentration are not considered in the model. The sensitivity analysis for assessing single plant and soil parameters taking part in K uptake, showed that only an increased K concentration in soil solution could bridge the gap between measured and calculated uptake. This led us to the conclusion that plants are able to mobilise K chemically.

Desorbing the sandy clay loam soil, used throughout this study, using different concentrations of citric and malic acids, which simulate root exudates, in $CaCl_2$ solution, showed that citric acid was more effective in desorbing K as compared to malic acid and the control.

Zusammenfassung

Pflanzenarten, aber auch verschiedene Sorten einer Pflanzenart unterscheiden sich z.T. sehr weitgehend in ihrer Kalium-Effizienz. Die Untersuchungen wurden durchgeführt, um ein tieferes Verständnis für die hierfür relevanten Mechanismen bei verschiedenen Pflanzenarten zu erlangen.

Hierzu wurde eine Serie von Gefäßversuchen unter kontrollierten Bedingungen in der Klimakammer und ein Feldversuch durchgeführt. Dabei wurden eine Vielzahl von Pflanzen- und Bodenparametern erhoben. Es wurde herausgefunden, dass sich die untersuchten Pflanzenarten sowohl in ihrer K-Effizienz als auch hinsichtlich der hierfür relevanten Mechanismen unterscheiden.

Die bei verschiedenen Arten gefundenen Mechanismen lassen sich wie folgt charakterisieren: ein geringer interner K-Bedarf der Pflanze, d.h. eine hohe K-Verwertungseffizienz; ein niedriger Nährstoffbedarf an der Wurzel aufgrund geringer Wachstumsraten des Sprosses und/oder eine hohe Aufnahmeeffizienz bedingt durch die Wurzelmorphologie. Hierzu gehört beispielsweise ein ausgedehntes Wurzelsystem, die Ausbildung von Wurzelhaaren und/oder die physiologische Aktivität des Wurzelsystems charakterisiert durch eine hohe Aufnahmerate pro Einheit Wurzel und Zeit.

Die Untersuchungen deuten auf eine mögliche Mobilisierung von Kalium durch die Wurzel einiger Pflanzenarten hin, lassen aber auch eine physiologische Anpassung an Bedingungen niedriger K-Konzentration in der Bodenlösung im Verlauf der Pflanzenentwicklung erkennen.

Für ein besseres Verständnis der der Nährstoffaufnahme verschiedener Pflanzenarten zugrunde liegenden Prozesse wurde der K-Transport im Boden und die Aufnahme durch die Pflanze mit einem mechanistischen Nährstoffaufnahmemodell unter Einbeziehung der Wurzelhaare berechnet. Die Ergebnisse zeigen, dass das Modell die Prozesse des K-Transports und der Aufnahme unter den Bedingungen ausreichender K-Versorgung richtig beschreibt. Bei K-Mangel wurde die tatsächliche Aufnahme jedoch über- oder auch unterschätzt. Die Überschätzung war bedingt durch die falsche Abschätzung der Aufnahmekinetik. Wohingegen die Unterschätzung der Aufnahme durch im Modell nicht berücksichtigte Mobilisierungsprozesse bedingt war. Sensitivitätsanalysen zeigen, dass nur eine erhöhte K-Konzentration in der Bodenlösung die Differenz zwischen

gemessener und berechneter Aufnahme erklären kann. Dies hat zu der Schlußfolgerung geführt, dass Pflanzen Kalium chemisch mobilisieren können.

In weiteren Untersuchungen wurden organische Säuren in $CaCl_2$-Lösung als synthetische Wurzelexsudate zur Desorption von Kalium verwendet. In einem sandigen Tonboden erwies sich dabei Citrat als gegenüber Malat sehr effektiv.

" Der Wunsch ist der Vater des Gedankens"
William Shakespeare

Contents

Chapter 1

General Introduction

Introduction

The demand for increased food production is concomitant to the continued growth of the world population. The severity of food shortage is especially serious, in the so-called developing countries, in Africa, Latin America and Asia (Chapin, 1987). In most of these countries, agriculture is faced with major problems of low soil fertility where semiarid, saline and calcareous soils constitute a large proportion of the land. Moreover, soil fertility is further threatened by cultivation practices such as continuous cropping, irrigation problems and soil erosion (Sauerbeck and Helal, 1990). Nevertheless, food demand must be met, consequently, crop cultivation expanded into marginal areas for crop production with regard to nutrient elements and water supply. Low productivity could be overcome to some extent by the use of high-yielding cultivars, however, such cultivars have large nutrient demand which can not be met under the soil conditions described previously. Soil fertility could be improved by adding fertilisers, a choice which is very restricted by the lack of enough capital and fertilisers availability. The low availability of nutrient elements due to fixation, for example, of phosphorous in calcareous soils (Sauerbeck and Helal, 1990) leads to reduced fertiliser efficiency. Unlimited chemical fertiliser use and decreased fertiliser efficiency present serious hazards to the environment through water and air pollution. A promising alternative could be the use of nutrient efficient cultivars. Use of these cultivars could be one of the major components contributing to land use systems, which enable maximum output with minimum input, sustain resources and conserve the environment. Growing nutrient-efficient species or cultivars could mean more efficient soil nutrient and fertiliser use as well as an environmental protecting approach which minimises the use of chemicals, and introduce a strategy of "tailoring the plant to fit the soil" (Rengel, 1999).

Nutrient efficiency

It is now recognised that various species and cultivars within a species vary widely in their ability to thrive in nutrient-deficient environments, indicating that plants differ greatly in their nutrient efficiencies (Jianjun and Gabelman, 1995; Cakmak et al., 1997; Fageria et al., 2001). There is much controversy concerning the concept of nutrient efficiency. However, definitions of nutrient efficiency are based on those emphasising productivity and those emphasising internal nutrient requirement

(Gourley et al., 1994). Considering yield parameters, efficiency with regard to a specific mineral nutrient, is the ability of a species or cultivar to produce a high yield, in a soil limiting in this particular nutrient element for a standard species or cultivar (Buso and Bliss, 1988). Agronomic efficiency is the total harvestable product per unit nutrient applied (Sauerbeck and Helal, 1990; Caradus, 1990). External efficiency or requirement is the nutrient content in the soil necessary to produce a certain portion, for example, 90% of maximum yield (Föhse et al., 1988). Another measurement of nutrient efficiency is the yield response per unit of added nutrient (Blair, 1993). Nutrient efficiency related to utilisation is the dry matter produced per unit nutrient element in the dry matter (Godwin and Blair, 1991). It is equivalent to the reciprocal of the nutrient concentration in the entire plant, often termed as the nutrient efficiency ratio (Gourley et al., 1994). Other workers used nutrient uptake efficiency (Claassen and Jungk, 1982; Buso and Bliss, 1988). Uptake efficiency is defined in terms of total uptake per plant or specific uptake per unit root length (Marschner, 1995). It is related to morphological root characteristics such as root system size and root diameter, which mean an increased root surface per unit of root weight, and root hairs, which allow for efficient nutrient scavenging of a larger soil volume. The second component of the uptake efficiency is the root physiological activity such as differing uptake kinetics, that is maximum uptake (I_{max}), Michaelis Menten kinetics (K_m) and minimum soil solution nutrient concentration (C_{Lmin}), which result in different nutrient uptake rates per unit root and time (Steingrobe and Claassen, 2000). Other mechanisms, which affect the specific uptake efficiency include, chemical mobilisation of nutrients by root exudates, induced pH changes in the rhizosphere and vesicular-arbuscular mycorrhizal (VAM) associations (Marschner, 1995).

Nutrient-efficient species, possess either morphological or physiological characteristics that facilitate higher nutrient uptake and/or better nutrient utilisation, or are able to chemically influence the rhizosphere with a consequent improved nutrient availability (Sattelmacher et al., 1994). Such species are useful in minimising leaching loss of, for example, NO_3^-, which may be found in the soil in plant available form, and are of paramount importance for taking up such nutrients, which are present in large total amounts in the soil, with relatively small plant available fractions and low concentrations in the soil solution, for example, P, K, Fe, Zn, Cu and Mn (Rengel, 1999).

Potassium fractions in soil

Potassium is one of the most abundant mineral elements and widely distributed constituent of the surface rocks of the earth, making up an estimated 2.6% of the earth's crust by weight, mostly present in minerals classified as feldspars and micas (Black, 1957). Feldspars occur exclusively in sand and silt fractions and to some extent in coarse clay. The micacious biotite and muscovite occur mainly in sand and silt, whereas illite is the main potassium-bearing mineral in the clay fraction of the soil. Except for illite which is of secondary origin, the other mentioned minerals could be of primary or secondary origin (Black, 1957). In feldspars K is imbedded in a crystalline aluminosilicate structure in which the K atom is surrounded and bonded to oxygen atoms. Each K atom is isolated from other K atoms by the bonds in the aluminosilicate part of the crystal structure, extending to completely surround each K atom. Potassium in micas is embedded in a crystalline aluminosilicate structure, but the K atoms lie in planes between molecular aluminosilicate network. Each K atom is surrounded by and bonded to oxygen atoms, however, the aluminosilicate layers are bonded together through the potassium ions by two separate sets of bonds, with each set in the molecular aluminosilicate layer on either side of the K. Potassium is found in soil in different forms with different solubility, depending on whether it is un-specifically electrostaticly bound to the soil colloids or specifically bound in the interlayer of clay minerals (Martin and Sparks, 1985). Hence, potassium is found in the soil liquid phase as exchangeable K, which is un-specifically bound, as fixed K, which is in the interlayer of 3-layer clay minerals specifically bound fraction and matrix-bound K, which is part of the crystals building minerals. The different fractions are also characterised by their extraction method, hence, the fraction which is released by repeated extraction with a 1 M ammonium acetate solution (pH 7), represents the exchangeable K and the remaining fractions represent non-exchangeable K (Scheffer and Schachtschabel, 1998). Depending on the soil type, climate and fertilisation level, adsorbed or readily exchangeable K is only around 100-1000 kg K ha^{-1}. The K concentrations in the soil solution are mostly in the range of 2-20 mg L^{-1}. The different K fractions are in equilibrium as: K in solution ↔ exchangeable K ↔ non-exchangeable K, where the equilibrium between the K in solution and exchangeable K is relatively more quickly established than that between exchangeable and non-exchangeable K (Scheffer and Schachtschabel, 1998). Generally soils rich in clay, and depending on their vermiculite and illite content, tend to render water soluble and exchangeable K into a non-exchangeable form, this phenomenon is called "K fixation". It indicates a decrease in the extractability of potassium as a result of interaction of originally soluble or extractable potassium with a soil or mineral (Black, 1957). Three soil characteristics have been found significant with regard to potassium fixation. It increases with: 1) clay content 2) increasing pH (Schachtschabel and Köster, 1960; Kaila, 1965). The third property is the degree of potassium saturation of the cation exchange capacity (CEC), where K fixation is little or non-existent in soils having a potassium saturation exceeding about 4.5%, while those with potassium saturation below about 4% have an increased K fixation (Chaminade, 1936). Potassium fixation is higher in sub-soil as compared to surface soil. In the field K is fixed after an extreme drying of the soil. Potassium fixing is extremely high in clay and loam soils, with expanded 3-layer clay minerals having high charge and low exchangeable K. Such soils are formed from river sediments and are rich in fine clay particles (<0.2 µm). They are formed as a result of the weak transport momentum of the flowing water (Scheffer and Schachtschabel, 1998).

Potassium efficiency

Several researchers reported that plant species differ in their K efficiency (Gardiner and Christensen, 1990; Meyer, 1993; Jianjun and Gabelman, 1995; Trehan and Claassen, 1998; Zhang et al., 1999; Steingrobe and Claassen, 2000; Fageria et al., 2001). Plant species take up considerable amounts of non-exchangeable K, which is the K fraction not extractable by ammonium acetate (Schachtschabel, 1937; Kuchenbuch and Jungk, 1984). However, plant species vary greatly in their ability to acquire non-exchangeable K due to variations in their root morphological and physiological characteristics (Mengel and Steffens, 1985). Therefore, efficient plant species, which are able to make use of the normally not readily available K, could have a significant agronomic importance. Differing K uptake efficiency of plant species was reported for plants grown in nutrient solution (Meyer, 1993; Trehan and Claassen, 1998), and for plants grown in the soil (Fageria et al., 2001), indicating that K uptake depends on plant and soil factors. This is to be expected, since nutrient uptake by plants from the soil results from interactions occurring at the soil-root interface (Claassen et al., 1986). It is a complex sequence of steps including desorption of ions from the solid phase, movement of nutrients towards the absorbing root, transport of ions through the membranes of the root cells towards the root xylem vessels and transport to the shoot (Claassen and Steingrobe, 1999). As such it is influenced by various soil and plant parameters and their interactions.

Soil and plant parameters related to K uptake from soil

Potassium concentration in the soil solution is often low (Rengel, 1993). As such mass flow, which depends on the water flux and concentration in the soil solution, plays a minor role in K nutrition of plants (Claassen, 1994), and K transport to the roots by diffusion is a quantitatively important process. Hence, soil factors which influence transport play a decisive role in K uptake by plants. The diffusive flux depends on the effective diffusion coefficient (D_e) and the concentration gradient. The effective diffusion coefficient depends on the diffusion coefficient in water (D_L), the buffer power (b), the volumetric water content (Θ) and the tortuosity factor (f). The concentration gradient depends on the difference between the concentration at the root surface (C_{L0}) and the soil solution concentration (C_{Li}) (Claassen and Steingrobe, 1999). Plant factors which influence K uptake include root morphological characteristics such as the root radius (r_0) and root hairs, which increase the root surface area and lead to more efficient K exploitation from a larger soil volume, and the physiological root activity described by the uptake kinetics: I_{max}, K_m and C_{Lmin} (Jungk and Claassen, 1997).

Furthermore chemical mobilisation of nutrients by plant roots, for example, by root exudates or their interactions with micro-organisms may be important for nutrient uptake efficiency (Marschner et al., 1986; Rengel, 1999).

Simulation models for nutrient uptake from soil

Nutrient simulation models are useful to improve our understanding of the processes governing soil supply and plant uptake of mineral nutrients. Two general categories of models are recognised (Rengel, 1993). Empirical models (Yerokun and Christenson, 1990), which describe observed phenomena by statistical means and regressions without trying to explain how they happen. They describe input-output relations not taking into account the underlying processes and as such are often called "black-box" models (Claassen and Steingrobe, 1999). Empirical models are suitable for practical objectives, since they employ a low number of easily obtainable parameters and the results are sufficient for practical use. The other category includes the mechanistic models (Nye and Marriot, 1969; Claassen and Barber, 1976; Cushman, 1979; Claassen et al., 1986; Claassen, 1994), which try to explain observed phenomena by means of basic biophysical, biochemical and physiological mechanisms, and mathematical description of the underlying processes and as such are more suited for scientific use (Rengel, 1993; Claassen and Steingrobe, 1999). Mechanistic models allow for the understanding of the underlying processes, whereby ideas can be proved, improved or rejected. They enable testing the correctness of our concepts about the interactions between plant and soil with regard to nutrient uptake by comparing modelled and observed results, where a lack of agreement shows areas in which more information and research is needed. Moreover, mechanistic models are valuable means for gaining access to calculating not easily measurable data such as nutrient concentration at the root surface, and for calculating the nutrient uptake from soils as affected by the involved soil and plant factors. By conducting a sensitivity analysis, where only a single input parameter is changed, it is possible to quantify the significance of individual soil and plant factors influencing uptake of a specific nutrient (Claassen et al., 1986; Rengel, 1993; Claassen and Steingrobe, 1999).

To simulate K uptake by the different plant species studied in the scope of this research, the model (NST) of Claassen (1994) which encompasses nutrient uptake by root hairs as well, is used. The model is based on three steps or processes: a) release of nutrients from the solid phase into the soil solution, b) transport of nutrients to roots in the soil liquid phase by mass flow and diffusion (Barber, 1962), c) nutrient uptake into the root which is dependent on the nutrient concentration in the soil solution at the root surface, and can be described by a modified Michaelis-Menten equation derived from enzyme kinetics, and applied by Epstein and Hagen (1952) and modified later by Nielsen (1972).

Chemical K mobilisation

Plant species with increased capacity to render sparingly soluble nutrient forms into plant available ones, or with a higher capacity to transport nutrients across the plasma membranes are considered to possess a high nutrient uptake efficiency (Rengel, 1999). However, if the rate of nutrient replenishment at the root surface is much lower than the capacity of the root cells to take up nutrients, uptake will be governed by the nutrient supply rather than by the nutrient uptake capacity of the root cells (Rengel, 1993). Hence, greater uptake capacity of the root cells such as high affinity nutrient uptake systems, would have an insignificant contribution to higher uptake efficiency for diffusion-supplied nutrients, for example, P, K, Zn, Mn and Cu (Rengel, 1999). Therefore, it could be concluded that a high capacity to increase nutrient solubility of normally sparingly soluble nutrients is an important mechanism for efficient nutrient uptake.

Chemical mobilisation of mineral nutrients in the rhizosphere by plant roots can play a decisive role in the acquisition of both anions, for example, phosphate and cations, for example, Fe, Cu and Zn (Marschner et al.,1986; Gerke, 1993; Gerke et al., 1994; Beißner and Römer, 1998; Rengel et al., 1998). Chemical mobilisation of nutrients in the rhizosphere is reported to be caused by the presence of micro-organisms, their interactions with plant roots and/or their exudates, changes in the pH through H^+ release which is related to increase in cation/anion uptake ratio, and to root exudates, which constitute of both high molecular weight exudates such as mucilage and ectoenzymes and low molecular weight exudates such as organic acids, sugars, phenolics and amino acids (Marschner, 1995). Very little information exists in the literature concerning chemical mobilisation of K by root exudates. Nevertheless, evidence shows that K deficient plants exude particularly organic acids in higher quantities in comparison to K sufficient plants. Kraffczyk et al. (1984) reported that no effect of K nutrition on the total quantity of exuded organic acids was detected, however, malic acid increased with increasing K supply, whereas oxalacetic acid and citric acid dominated at low K supply. Citric acid, in concentrations analysed in the rhizosphere of the proteoid roots of white lupine, reportedly enhanced release of interlayer bound K (Steffens and Zarhoul, 1997), from loess soil (Meyer, 1993) and from different clay minerals (Song and Huang, 1988). As mentioned above plant species utilise non-exchangeable K or interlayer K to varying degrees. The mechanism by which K is released from the interlayer of clay minerals are not clearly known. Some workers suggest that extreme K depletion at the root surface to concentrations as low as 2-3 µM initiates release of non-exchangeable K from interlayer positions of clay minerals (Claassen et al., 1981; Springob and Richter, 1998). Hinsinger et al. (1992) proposed that due to root depletion of rhizosphere K by 4 days old ryegrass roots, grown on phlogopite embedded in agar, the exchange equilibrium was shifted with the resulting release of interlayer K and expansion of the interlayer space of the mineral. Kuchenbuch (1983) suggested exuded H^+ which exchange for K as the cause for the release of non-exchangeable K. Evidence exists that plant roots cause acidification in the rhizosphere by light dependent active excretion of H^+ (Mengel and Malissiovas, 1982). The authors found significantly higher H^+ excretion under light conditions than in the dark. Accordingly plants growing under high light intensity, for example, in the field probably excrete higher amounts of H^+ under the influence of the higher light intensity. The excreted H^+, probably accompanied by passive release of anions, inorganic or organic, must be of vital significance for many reactions going on in the rhizosphere (Mengel and Malissiovas, 1982). On the other hand, Springob and Richter (1998) showed that above pH 4, H^+ have a negligible effect on release of non exchangeable potassium. The formation of metal organic complexes by the OH^- and $COOH^-$ groups of the low molecular weight organic acids with the metal ions Al, Fe and Mg of the mineral structures such as clay minerals, which results in an acceleration of the decomposition of the minerals and, consequently, K release from the interlayer clay minerals, was given as a possible mechanism by Song and Huang (1988).

Aim of the research and outline of the thesis

This research was conducted with the objective of studying K efficiency of plants and K dynamics in the rhizosphere of different plant species, both under controlled (pot experiments) and natural (field experiment) conditions, on different soil types. Another objective was a closer investigation of the possible mechanisms behind the different K efficiency of the studied species, and studying K dynamics in the rhizosphere by simulating K uptake using a mechanistic model.

In Chapter 2 is a study based on a pot experiment with 14 different plant species grown on humic sandy soil under controlled conditions, for evaluating K efficiency and selecting plants with different efficiencies for further studies.

In Chapter 3 K efficiency of 3 plant species with differing efficiency mechanisms was studied. The plant species were studied in a pot experiment in a K “fixing” soil, under controlled conditions with different K concentrations in the soil solution, ranging from deficient to optimum levels.

Chapter 4 represents evaluation of K efficiency of 2 plant species with differing efficiency mechanisms under field conditions on a K fixing soil.

Potassium uptake by plants was simulated by a mechanistic model (Claassen, 1994) in Chapter 5. This study allowed for understanding the K dynamics in the rhizosphere, and enabled the comparison between actually measured and calculated K uptake, which showed the possible mechanisms that could be behind the varying K efficiency of the studied plant species. Also significance of individual plant and soil parameters involved in K uptake were assessed by conducting a sensitivity analysis. In Chapter 6 the possibility of chemical mobilisation of K in a "K-fixing " soil by organic acids, in concentrations found in the rhizosphere of stressed plants, was investigated.

The thesis concludes in Chapter 7 with a general discussion of the results, evaluation of the findings of the research and out-lining prospects for future research.

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Chapter 2

Potassium Efficiency of 14 Different Plant Species Grown on a Sandy Soil

Abstract

Plant species and cultivars within a species differ in their K efficiency. Differences in efficiency could be due to differences in uptake efficiency characterised by morphological and/or physiological root parameters, to the growth rate of shoots and/or to differing utilisation efficiency.

The goal of this study was to select plant species with differing K efficiency and determine plant parameters affecting efficiency for further studies. The study was carried out using 14 different plant species and cultivars grown on a sandy soil rich in humus, with 2 K fertilisation levels under controlled conditions.

The studied plant species and cultivars showed differing K efficiency reflected in different dry matter yield production on unfertilised relative to fertilised treatments. All species had at low K supply, less than optimum K concentration in dry matter, indicating that the soil K concentration did not meet the external K requirement of the plants. Thus species able to produce higher dry matter yield indicated superior adaptability to K deficiency. The efficiency mechanisms employed by the different species were either low shoot growth rate and/or high root length - shoot weight ratio, a high uptake rate per unit root, that is the influx, or low internal K requirement. Differences in influx by the different species could have been caused by differing physiological activity of the roots. As was shown by model, calculations species with high influx had higher calculated concentration gradients, since they caused further decrease of the concentration at the root surface, thus creating steeper concentration gradients between bulk soil solution and root surface which resulted in higher diffusive flux to the roots.

The much higher K concentrations measured in soil solution of some species which, nevertheless, were not able to grow well, could have been caused by problems in measuring K in soil solution. That is K was not actually in the solution, instead on fine soil particles dispersed in the soil solution and was measured by the flame emission. Dispersion of soil particles might have been enhanced by root exudates.

Introduction:

It is now well known that plant species and even cultivars within a species differ in their nutrient efficiency (Cakmak et al., 1997). Efficient species or cultivars are those able to grow and yield well when growing under deficiency conditions as compared to inefficient species. Several workers found varying K efficiency among different plant species and genotypes. For example, Sadana and Claassen (1999) showed in a pot experiment with young plants, that sugar beet was more K efficient than wheat and maize. Jianjun and Gabelman (1995) testing 100 different tomato strains, isolated tomato strains which were more K efficient than others. Efficient species have either certain morphological or physiological characteristics that increase uptake or utilisation of nutrients, or are able to chemically change the rhizosphere to improve the availability of nutrients (Sattelmacher et al., 1994). Hence, reasons for varying K efficiency could be due for one, to variations in internal requirements or use efficiency (Gardiner and Christensen, 1990; Trehan and Claassen, 1998). The internal requirement is the K concentration in plants needed to produce a certain proportion of the maximum yield, for example, 90% as used by Föhse et al. (1988). Other reasons for efficiency could be the K uptake ability of the plants, that is acquiring K from the soil or solution and accumulating it in the shoots. This depends on the amount of roots and on the efficiency of the single roots to take up K or the influx.

Hence, one of the major components contributing to land use systems, which enable maximum output with minimum input, sustain resources and conserve the environment, could be the use of efficient plant species (Rengel, 1999). Accordingly species which are able to make use of the normally not readily available K could have a significant agronomic importance.

The objective of this study was to select plant species with differing K efficiency and determine plant parameters affecting efficiency for further studies. To achieve this goal 14 different plant species were tested in a pot experiment with 2 K fertilisation levels under controlled growth conditions.

Materials and Methods

Table 1 shows the different plant species used in the experiment, plants per pot and harvest times.

The plants were grown in a growth chamber with a day/night regime 16/8 hours, temperature of 25/15 °C for cotton and maize and 20/15 °C for all other species and relative humidity 70%. The photosynthetic active radiation during the day time was 250 µE m^{-2} s^{-1}.

Plastic pots of 1.2 L capacity were filled with 1.2 kg sandy soil rich in humus from Hodenhagen North Germany, having pH ($CaCl_2$) 5.2, 3 % clay, 7 % silt, 5.5 % humus and 537 µmol kg^{-1} soil exchangeable K. Two K levels 0 and 300 mg pot^{-1} were added as KCl. Other nutrients were added per pot as follows: 200 mg N as NH_4NO_3, 50 mg Mg as $MgSO_4.7H_2O$, 200 mg P as Ca $(H_2PO_4)_2$. The plants were watered daily to 20% by weight. Two pots per treatments were left un-planted as control. Each treatment was replicated twice.

Shoots

At harvest the plants were cut at the soil surface, after fresh weight determination, the dry weight was determined by drying the plants at 105 °C till constant weight. The samples were then finely ground for chemical analysis.

Plants Chemical analysis

Sub-samples of the ground plant material were wet digested in a concentrated tri acid mixture (HNO_3, $HCLO_4$, and H_2SO_4 in a volumetric ratio of 8:2:1, respectively). Potassium concentration was determined by flame photometry.

Table 1 *Plant species, time between sowing, first and second harvest and the number of plants per pot*

Plant species	Time until harvest (days)		Number of plants pot^{-1}	
	t_1	t_2	1st harvest	2nd harvest
Spring Wheat *Triticum aestivum* L. cv. Star	15	32	4	4
Spring Barley *Hordeum vulgare* L. cv. Marina	15	32	4	4

Table 1 (cont.)

Winter Wheat *Triticum aestivum* L. cv. LPI 601	15	32	4	4
Winter Barley *Hordeum vulgare* L. cv. Trasco	15	32	4	4
Rye grass *Lolium perenne* L. cv.Locarno	14	34	4	4
Oilseed rape *Brassica napus* L. cv. Liraget	16	34	2	2
Sugar beet *Beta vulgaris* L. cv. Aries	16	34	3	3
Sunflower *Helianthus annus* L.	17	34	3	3
Maize *Zea mays* L. cv. Konsul	14	34	4	4
Maize *Zea mays* L. cv. Ferris	14	34	4	4
Spinach *Spinacea oleracea* L. cv.Subito RZ	17	34	3	3
Faba beans *Vicia faba* L. cv. Victor	17	32	4	3
Elephant grass *Pennisetum purpureum* L.	16	34	4	3
Cotton *Gossypium barbadense* L.	15	32	4	4

Root length (RL), and root radius (r_0)

The roots in the whole pot were separated from the soil by washing them gently over a 0.2 mm sieve. The water remaining on the roots was removed by a 10 minute centrifugation at 1200 rev. min^{-1}. After determining the root fresh weight, the root length was measured on representative sub-samples of 0.2 -0.5 g depending on the plant species and age. The sub-samples were kept in 20 % ethanol.

The root length was measured using the line intersection method (Newman, 1966). Here the roots of the sub-sample were cut in approximately 0.5 cm pieces and were distributed evenly over a 0.2 mm sieve with 314 cm^2 surface area which is placed under a microscope. The sieve is then pushed 100 times randomly, and the root segments intersecting with a hairline in the ocular were counted. The root length of the sub-sample is calculated using the following equation:

$$RL = \frac{\pi N F}{2 n H} \qquad [1]$$

where:

N = Sum of the intersections of all the measurement
F = Sieve surface area (cm^2)
n = Count number
H = Hairline length (cm)

The sub-sample related to the total root fresh weight gives the total root length.

The mean root radius was calculated using the following equation with the assumption that the specific weight of roots is 1 g cm^{-3}:

$$r_0 = \sqrt{\frac{RFW}{\pi RL}} \quad (cm) \qquad [2]$$

where:

RFW = root fresh weight (g)
RL = root length (cm)

Root Length density (RL_v)

This is the root length per unit soil volume, it is given by dividing the total root length (RL) by the soil volume of the pot (SV):

$$RL_v = \frac{RL}{SV} \quad (cm\ cm^{-3}) \qquad [3]$$

Average half distance between neighbouring roots (r_1)

Assuming that the roots are regularly distributed in the soil, the average half distance between neighbouring roots was calculated using the root length density RL_v:

$$r_1 = \sqrt{\frac{1}{\pi RL_v}} \qquad \text{(cm)} \qquad [4]$$

Extension of the depletion zone (Δx)

Was calculated as follows (Syring and Claassen, 1995):

$$\Delta x = \sqrt{\pi D_e t} \qquad [5]$$

where

D_e is the effective diffusion coefficient

t is the time between the first and second harvest .

Relative Growth rate (RGR_s)

The relative shoot growth rate (RGR_s) was calculated using the following equation:

$$RGR_s = \frac{\ln\left(\frac{SW_2}{SW_1}\right)}{t_2 - t_1} \qquad [6]$$

where:

SW = shoot dry weight (g)
t = time (days)

the indices 1 and 2 represent the first and second harvest.

The influx (In)

The influx is the net amount of a nutrient element taken up by the plant per unit root length or surface area and time. A direct measurement of the influx is not possible, therefore, only an average influx can be calculated for a given time period. For calculating the influx, at least two harvests are needed in which the nutrient content and root length of the plants are known. Assuming that the young plants have an exponential growth, the influx was calculated after Williams (1948),

$$\mathrm{In} = \frac{U_2 - U_1}{t_2 - t_1} \frac{\ln\left(\frac{RL_2}{RL_1}\right)}{RL_2 - RL_1} \qquad [7]$$

where

U = nutrient element content in the plant (mol)

RL = root length (cm)

t = time (s)

the indices 1 and 2 represent the first and second harvest.

Concentration difference between bulk soil and root surface (ΔC_L)

This is the difference in K concentration between bulk soil solution and concentration at the root surface needed to drive a given flux by diffusion. This flux is given by the influx (In). ΔC_L was calculated as follows (Barraclough, 1986):

$$\Delta C_L = \frac{\mathrm{In}}{4\pi D_L \Theta f}\left(1 - \frac{1}{1 - \pi r_0^2 RL_v} \ln \frac{1}{\pi r_0^2 RL_v}\right) \qquad [8]$$

where

D_L = K diffusion coefficient in water ($cm^2\ s^{-1} = 1.98 \times 10^{-5}$)

Θ = volumetric water content ($cm^3\ cm^{-3}$)

f = impedance factor after Kaselowsky (1990)

r_0 = root radius (cm)

RL_v= root length density ($cm\ cm^{-3}$)

Soil Analysis

Soil solution

The soil solution was obtained by a modified displacement technique of Adams (1974), whereby a 250 mL cylinder with a filter paper covering an opening on the bottom, was filled with moist soil. Using a peristaltic pump, water was allowed to drop slowly on the soil, displacing the soil solution downwards, where it is taken in glass beakers. To exclude soil solution dilution by the added water, 4% potassium thiocyianate was added as a marker to the water and the soil solution obtained was then tested with 5% $FeCl_3$. A red coloration in the solution indicated the presence of the marker. With repeated measurements, the marker was not detected in a solution volume below 10 mL, hence, the first 5 mL of soil solution were taken for potassium concentrations measurement. The K concentration was determined by flame photometry.

Exchangeable potassium and pH

One g field moist soil is weighed in a filter paper placed on a funnel. The soil was extracted 5 times with 10 ml 1 M NH_4OAc solution (pH 7) at 15 minutes intervals. The K concentration in the extract was determined by flame photometry. The soil exchangeable K content was calculated on dry weight basis.

The pH value was measured in 0.01 M $CaCl_2$ in a 1:2.5 soil:solution ratio. Soil samples were dried at 105^oC to constant weight and the gravimetric water content determined.

Statistical Analysis

The data were statistically analysed using analysis of variance (ANOVA), where significant differences were found, mean separation was conducted using the Tukey test.

Results

Relative and absolute dry matter yield

Table 2 shows the dry matter yield of the different plant species with and without K fertilisation, dry matter yield of unfertilised relative to fertilised treatments and percent K concentration in the dry matter as affected by K fertilisation. Potassium efficiency of the different plant species, expressed as the shoot dry matter yield of the unfertilised relative to the fertilised treatments, was highest for spring wheat (51 %) and least for spinach (15 %). Relative yield differed significantly ($p \leq 0.001$) among different plant species. Mean dry weight of the plant species, in mg plant^{-1}, ranged between 72 to 1000 under low K, and 183-4003 under adequate K supply (Table 2). Some of the plant species, namely, barley, both maize cultivars, sunflower, oilseed rape and spinach showed visual K deficiency symptoms on unfertilised treatments, especially spinach was severely affected.

Potassium concentration in dry matter

Potassium concentration in the dry matter is a measure for the nutritional status of the plant. Plant species differ in their internal K requirements, which is the K concentration needed for producing, for example, 90% of maximum yield. Percent K concentration in dry matter ranged between 0.31 to 1.09 % for the unfertilised and 1.76 to 8.10 % for the fertilised treatments (Table 2). The maize cultivars had the least K dry matter concentration on both treatments, whereas elephant grass, spinach and sugar beet had the highest K concentration on the unfertilised and fertilised treatments, respectively.

Table 2 *Dry matter yield, relative yield and K concentration in the dry matter of 14 different plant species grown on a sandy soil without (-K) and with (+K) K fertilisation*

	Dry matter yield		Relative yield	K conc. in dry matter	
Plant species	- K	+ K [ψ]		- K	+ K
	mg plant^{-1}		%		
Spring wheat	264 (0.04)	521 (0.82)	51 (2.2)	0.75 (0.02)	5.08 (0.03)
Spring barley	331 (0.07)	974 (0.12)	34 (3.0)	0.48 (0.01)	4.79 (0.15)
Winter wheat	286 (0.03)	751 (0.09)	38 (2.4)	0.66 (0.03)	4.99 (0.05)
Winter barley	263 (0.05)	1004 (0.02)	26 (1.4)	0.52 (0.03)	4.97 (0.16)
Winter rye	386 (0.02)	1039 (0.05)	37 (0.8)	0.51 (0.01)	4.40 (0.21)
Oilseed rape	455 (0.13)	2415 (0.32)	19 (3.9)	0.48 (0.01)	3.71 (0.31)
Sugar beet	125 (0.20)	449 (0.11)	28 (3.8)	0.70 (0.02)	8.10 (0.13)
Sunflower	425 (0.11)	1555 (0.42)	27 (0.0)	0.46 (0.01)	3.62 (0.60)
Maize Konsul	1000 (0.13)	4003 (0.22)	25 (1.2)	0.31 (0.01)	1.76 (0.12)
Maize Ferris	963 (0.06)	3620 (0.04)	27 (0.3)	0.31 (0.02)	1.98 (0.25)
Spinach	82 (0.03)	538 (0.16)	15 (3.8)	0.52 (0.01)	6.15 (0.12)
Faba bean	410 (0.01)	1587 (0.01)	26 (0.8)	0.52 (0.03)	3.42 (0.59)
Elephant grass	72 (0.01)	183 (0.03)	39 (1.2)	1.09 (0.02)	5.88 (0.22)
Cotton	518 (0.03)	1863 (0.19)	28 (0.3)	0.36 (0.03)	3.04 (0.06)
[φ]HSD (0.05)			12.6		

[ψ] The means of the fertilised treatment were significantly ($P \leq 0.001$) different from unfertilised treatment for all plant species.

[φ]Highest significant difference calculated after Tukey.

Values between brackets represent the standard error of means.

Root length-shoot weight ratio (RSR), root length density (RL_v), average half distance between neighbouring roots (r_1) and extension of the K depletion zone (Δx)

The amount of K taken up by a plant will depend on the root size and its distribution in the soil profile. Amount of K absorbed by each root segment will partly depend on the soil volume it can exploit, that is the distance to the neighbouring roots.

Table 3 *Relative shoot growth rate (RGR_s) and root shoot ratio (RSR) of 14 different plant species grown on a sandy soil without (-K) and with (+K) K fertilisation*

	Relative shoot growth rate		Root length-shoot weight ratio	
Plant species	- K	+ K$^{\Psi}$	- K	+ K
	d^{-1}		cm mg^{-1}	
Spring wheat	0.06 (0.01)	0.09 (0.03)	4.2 (1.03)	2.2 (0.32)
Spring barley	0.08 (0.01)	0.13 (0.01)	5.8 (0.32)	3.1 (0.68)
Winter wheat	0.07 (0.01)	0.12 (0.01)	4.3 (0.34)	5.3 (0.57)
Winter barley	0.06 (0.01)	0.13 (0.01)	2.9 (0.15)	11.0 (0.11)
Winter rye	0.08 (0.01)	0.12 (0.01)	2.7 (0.31)	4.2 (1.14)
Oilseed Rape	0.15 (0.01)	0.26 (0.03)	2.1 (0.33)	0.9 (0.27)
Sugar beet	0.15 (0.07)	0.23 (0.01)	4.4 (0.99)	5.2 (0.06)
Sunflower	0.12 (0.04)	0.16 (0.03)	0.9 (0.13)	3.6 (0.37)
Maize Konsul	0.15 (0.07)	0.21 (0.01)	1.8 (0.12)	4.9 (0.52)
Maize Ferris	0.16 (0.01)	0.22 (0.01)	2.6 (0.23)	4.4 (0.33)
Spinach	0.08 (0.03)	0.24 (0.06)	1.1 (0.15)	2.2 (0.23)
Faba bean	0.06 (0.01)	0.13 (0.01)	9.3 (0.37)	5.2 (0.80)
Elephant grass	0.09 (0.01)	0.19 (0.01)	2.4 (0.56)	2.5 (0.07)
Cotton	0.06 (0.01)	0.14 (0.01)	3.1 (0.27)	2.8 (0.55)
$^{\phi}$HSD (0.05)	0.09	0.12	5.2	6.7

$^{\Psi}$ The means of the fertilised treatment were significantly ($P \leq 0.001$) different from unfertilised treatment for all plant species.

$^{\phi}$Highest significant difference calculated after Tukey.

Values between brackets represent the standard error of means.

The root system is represented here by the RSR because it gives the amount of roots available to feed the shoot, by the RL_v, which shows the amount of roots per unit soil volume and the distance between neighbouring roots (r_1), which is an indication for possible inter-root competition. For the RSR (Table 3) no significant differences were found between fertilised and unfertilised treatments for all plant species, however, the latter interacted significantly with fertilisation ($p < 0.05$). Hence, both wheat cultivars, spring barley, oilseed rape, faba beans and cotton had higher RSR on unfertilised as compared to fertilised treatments, whereas the reverse was true for all the remaining species. The increase in root length-shoot weight ratio without fertilisation differed between the species, for example, while it was in the range of 3-4 folds for maize, winter barley and sunflower, it was in the range of 1-2 folds for elephant grass, spinach and sugar beet. Root length density (Table 4) differed significantly ($p \leq 0.001$) between plant species. It was highest for faba beans and maize cv. Ferris and least for spinach and elephant grass. Average half distance between neighbouring roots (r_1) ranged between 0.2-1.1 cm by the different species.

Table 4 *Root length density (RL_v) and the average half distance between the roots (r_1) of 14 different plant species grown on a sandy soil without K fertilisation*

Plant species	Root length density (RL_v)	Average half distance (r_1)
	cm cm^{-3}	cm
Spring wheat	4.4 (0.896)	0.3 (0.028)
Spring barley	7.7 (0.857)	0.2 (0.011)
Winter wheat	5.0 (0.545)	0.3 (0.014)
Winter barley	3.0 (0.306)	0.3 (0.016)
Winter rye	4.2 (0.546)	0.3 (0.018)
Oilseed rape	2.0 (0.576)	0.4 (0.061)
Sugar beet	1.8 (0.002)	0.4 (0.012)
Sunflower	1.2 (0.278)	0.5 (0.060)
Maize Konsul	7.1 (0.735)	0.2 (0.011)
Maize Ferris	10.2 (1.039)	0.2 (0.009)
Spinach	0.3 (0.002)	1.1 (0.003)
Faba bean	13.3 (0.840)	0.2 (0.026)
Elephant grass	0.5 (0.132)	0.8 (0.010)
Cotton	6.4 (0.646)	0.2 (0.011)
$^{\phi}$HSD (0.05)	7.1	0.2

$^{\phi}$ Highest significant difference calculated after Tukey.
Values between brackets represent the standard error of means.

All cereals had more or less similar r_1, which was intermediate for sugar beet, oilseed rape and sun flower and largest for spinach. The extension of the K depletion zone (Δx) is the distance to which K can be depleted around the roots. It is calculated from the effective diffusion coefficient (D_e) and the time difference between the 2 harvests (equation 5). The value of Δx was 0.24 cm for the plant species studied. This value was equal or smaller than r_1 value of all plant species indicating that no inter-root competition for K took place.

Relative shoot growth rate (RGR_s)

The rate at which shoots grow under optimum K conditions is related to the demand for the nutrient imposed on the roots. Hence, at the same RSR, plants with a high shoot growth rate indicate a higher nutrient demand on the roots and vice versa. Except for the 2 maize cultivars, all cereals as well as faba beans had low RGR_s (Table 3). In comparison oilseed rape and sugar beet had nearly double higher RGR_s with and without fertilisation. Spinach and elephant grass had even 3 and 2 times higher RGR_s on fertilised as compared to unfertilised treatments, indicating that on the latter treatments, K was limiting growth strongly. For the RGR_s highly significant differences were found between the fertilisation levels and between plant species ($p \leq 0.001$) but their interaction was not significant.

Total K uptake and influx

Table 5 shows the total K uptake and influx as affected by K fertilisation. The K uptake is a measure for the acquisition ability of the root system to supply plants with K. It varied significantly between the fertilisation levels ($p \leq 0.001$). Generally all plant species had a low K content on the unfertilised treatments. This means that for all plant species K uptake was limited by K supply by the soil. Both wheat cultivars, rye and cotton had more or less similar K content in dry matter without fertilisation. However, K content did not follow the same pattern on fertilised treatments. Elephant grass had the least uptake on both treatments (Table 5).

The influx which is the efficiency of the single roots to take up K, varied greatly among plant species both with and without fertilisation. Sunflower had the highest K influx on the unfertilised treatments followed by elephant grass and oilseed rape and it was least for winter barley. This indicates that as well as soil conditions, K influx depends on plant characteristics. On the fertilised treatments, oilseed rape had the highest influx followed by sugar beet, spinach and elephant grass. Least influx was found by maize cv. Konsul. Highly significant differences were found between the 2 fertilisation levels ($p \leq 0.001$).

Table 5 *Potassium content and influx of 14 different plant species grown on a sandy soil without (-K) and with (+K) K fertilisation*

	Plant K content		**K influx**	
Plant species	-K	+K$^{\Psi}$	-K	+K$^{\Psi}$
	μmol K pot^{-1}		10^{-14} mol cm^{-1} s^{-1}	
Spring wheat	201 (3.19)	2703 (53.8)	3.35 (1.04)	59.8 (19.2)
Spring barley	164 (5.23)	4780 (57.2)	1.01 (0.10)	56.2 (11.9)
Winter wheat	194 (7.99)	3832 (78.9)	1.48 (0.12)	34.4 (3.73)
Winter barley	140 (0.86)	5098 (84.5)	0.77 (0.15)	23.8 (0.64)
Winter rye	201 (7.46)	4674 (93.1)	3.79 (0.38)	46.8 (10.8)
Oilseed rape	111 (4.96)	4553 (78.8)	5.32 (1.61)	195.0 (18.2)
Sugar beet	80 (4.99)	2190 (74.3)	3.76 (0.69)	115.0 (20.1)
Sunflower	148 (5.83)	4250 (77.7)	9.98 (1.05)	48.9 (1.34)
Maize Konsul	316 (3.59)	7183 (91.3)	3.02 (0.33)	14.6 (0.65)
Maize Ferris	302 (7.97)	7333 (87.2)	2.62 (0.04)	21.0 (2.57)
Spinach	36 (4.22)	2544 (78.1)	2.85 (0.06)	79.7 (15.4)
Faba bean	162 (5.27)	4166 (65.9)	1.40 (0.55)	30.2 (3.09)
Elephant grass	63 (3.36)	909 (24.7)	9.07 (0.55)	62.9 (4.65)
Cotton	192 (7.81)	5794 (68.2)	3.03 (0.47)	39.1 (4.81)
$^{\phi}$HSD (0.05)	74	2668	5.05	114

$^{\Psi}$ The means of the fertilised treatments were significantly ($P \leq 0.001$) different from unfertilised treatment for all plant species.

$^{\phi}$ Highest significant difference calculated after Tukey.

Values between brackets represent the standard error of means.

Initial soil solution concentration (C_{Li}), root radius (r_0), concentration difference in soil solution (ΔC_L) needed to drive the given influx and concentration at the root surface (C_{L0})

The concentration difference, necessary for driving a diffusion flux towards the root in the same order as the measured average influx, can be calculated by equation 8. It depends mainly on the K influx and differed, therefore, greatly between the plant species (Table 6). The calculated values of ΔC_L for some species such as winter wheat, barley and faba beans were smaller than the C_{Li} and as such could explain the diffusive flux to the roots. However, the calculated ΔC_L values for some species such as sunflower, sugar beet and elephant grass were by far greater than the C_{Li} of the bulk soil. This indicates that some processes, which were not included in the calculation of ΔC_L, took place in the rhizosphere.

Table 6 *Initial K soil solution concentration of the bulk soil (C_{Li}), root radius (r_0), concentration difference in soil solution (ΔC_L) needed between bulk soil and the root surface to drive a given flux by diffusion and calculated concentration at the root surface (C_{L0}) of 14 different plant species grown on a sandy soil without K fertilisation*

Plant species	r_0	Δ C_L	C_{L0}
	10^{-2} cm	µmol L^{-1}	
Spring wheat	1.22 (0.021)	15.24 (0.48)	-0.15 (0.45)
Spring barley	0.96 (0.031)	4.50 (0.44)	10.59 (0.52)
Winter wheat	1.14 (0.005)	6.75 (0.61)	8.34 (0.11)
Winter barley	1.37 (0.026)	3.59 (0.08)	11.50 (0.35)
Winter rye	1.03 (0.018)	18.51 (0.58)	-3.42 (0.72)
Oilseed rape	1.24 (0.104)	27.69 (0.57)	-12.60 (0.41)
Sugar beet	1.12 (0.015)	20.60 (0.34)	-5.51 (0.22)
Sunflower	1.34 (0.035)	54.94 (0.37)	-39.85 (0.37)
Maize Konsul	1.34 (0.117)	11.98 (0.48)	3.11 (0.49)
Maize Ferris	1.36 (0.002)	9.52 (0.38)	5.57 (0.38)
Spinach	1.66 (0.029)	18.10 (0.30)	-3.01 (0.15)
Faba bean	1.82 (0.004)	4.08 (0.22)	11.01 (0.28)
Elephant grass	1.55 (0.129)	54.65 (0.54)	-39.56 (0.45)
Cotton	1.52 (0.120)	11.64 (0.17)	3.45 (0.67)

For all species (C_{Li}) = 15µmol L^{-1}.
For calculating (ΔC_L) (Eq. 8) the following parameters were used: (D_L) = 1.98 x 10^{-5} cm^2 s^{-1}, (Θ) = 0.25 cm^3 cm^{-3}, (f) = 1.58Θ -0.17, Influx (see Table 5) and RL_v (see Table 4).
Values between brackets represent the standard error of means.

Soil solution K concentration (C_{Li}) and exchangeable K (K exch.) at the final harvest

Soil solution K concentration after the harvest of plants varied strongly depending on the species that had grown in the soil (Table 7). Wheat and maize cultivars decreased the K concentration in the soil solution to around one third of the initial concentrations of the un-planted control (15 µmol L^{-1}). It is interesting to find that by some plant species such as sugar beet, spinach and elephant grass the K concentration in soil solution was up to 6 times the concentration found in un-planted soil (15 µmol L^{-1}).

Significant differences ($p \leq 0.001$) between the plant species were found in the decrease of exchangeable K (Table 7). Spring barley, winter wheat and maize cultivars lowered the exchangeable K to about half the initial concentration (20 µmol 100^{-1} g soil). Species such as elephant grass, spinach and sunflower decreased it by only around 10%.

Table 7 *Exchangeable K(exch. K) and soil solution K concentration after growing 14 different plant species on a sandy soil without K fertilisation*

Plant species	Exchangeable K	Soil solution K conc.
	µmol 100^{-1} g soil	µmol L^{-1}
Spring wheat	33.0 (0.64)	4.1 (0.27)
Spring barley	26.6 (0.62)	16.2 (0.13)
Winter wheat	25.3 (0.99)	2.6 (0.26)
Winter barley	30.6 (0.96)	15.5 (0.13)
Winter rye	36.6 (0.76)	23.8 (0.06)
Oilseed rape	33.3 (0.81)	22.0 (0.05)
Sugar beet	33.5 (0.38)	94.2 (0.15)
Sunflower	44.8 (0.26)	49.1 (0.12)
Maize Konsul	28.8 (0.91)	14.7 (0.41)
Maize Ferris	27.9 (0.52)	4.9 (0.52)
Spinach	44.9 (0.86)	89.8 (0.55)
Faba bean	37.7 (0.68)	28.1 (0.38)
Elephant grass	48.4 (0.43)	87.7 (0.41)
Cotton	29.7 (0.40)	10.2 (0.29)
Control (un-planted)	53.7 (0.67)	15 (0.08)
$^{\phi}$HSD (0.05)	20.1	76.7

C_{Li} = 15 µmol L^{-1} for all plant species.

$^{\phi}$ Highest significant difference calculated after Tukey.

Values between brackets represent the standard error of means.

Discussion:

Plants growing in pots under controlled conditions are not able to express their efficiency as do plants growing in the field, which are subjected to natural growth conditions such as variable temperature, high radiation and various soil chemical and physical reactions. All these factors could affect the physiological and morphological development of plants and thereby also plant performance. In pots, plants grow in a confined volume and the root system explores the whole pot with the result that the whole soil volume may supply nutrient to the plant.

Higher RL_v results in smaller average half distance between neighbouring roots (r_1). If r_1 is smaller than the extension of the ion depletion zone (Δx), this will in turn lead to overlapping of the depleted soil volume between neighbouring roots and inter-root competition occurs. Accordingly the flux towards the roots and, hence, the influx may also decrease (Meyer, 1993). However, in this study the plants were harvested relatively young and the root length density (RL_v) was comparable to those found in the field (Table 4). The value of Δx was either equal or smaller than r_1 values of all plant species. Hence, root competition probably was not the factor limiting K uptake.

In this study, the K efficiency expressed as the dry matter yield without fertilisation relative to maximum dry matter yield, differed greatly among the different plant species (Table 2). Potassium efficiency could be due to differences in internal requirement and/or uptake efficiency (Trehan and Claassen, 1998; Sadana and Claassen, 1999). For all tested plant species, K concentration in dry matter on the unfertilised treatments, was far below optimum internal concentration (Bergmann, 1993). For example, the optimum K concentration in dry matter for spring wheat lies between 3.3-4.5% and for sugar beet and spinach between 3.5-6 and 3.5-5.3%, respectively. In this study, at deficient K levels, the respective plant species were able to accumulate only 16, 12 and 10% of their optimum K requirement (Table 2). This indicates that the plant species were not able to accumulate enough K in the shoots. However, species with more relative yield indicated a superior capacity to adapt to the existing soil conditions. Therefore, species such as wheat could be said to have a high utilisation efficiency, since it was able to produce more relative yield with an internal K concentration which was much lower than the optimum level. Whereas spinach could be considered as having low use efficiency, since it was incapable of high dry matter production. This could have been because the very low

K concentration in the soil solution of the non fertilised treatments (15 µmol K L^{-1}), did not meet the external K requirements of the plants. External requirement is the nutrient content in the soil to produce a certain portion, for example, 90%, of maximum yield (Föhse et al., 1988).

The other reasons, which could explain varying plant responses to K deficiency, are the demand imposed on the roots by the shoots, RGR_s and the uptake efficiency. The latter depends on the root size, root length-shoot weight ratio (RSR) and uptake efficiency of each root segment or influx. Faster growing shoots have more need for nutrients and, therefore, impose higher demand on the roots (Sadana and Claassen, 1999). The dry matter production is determined by the shoot growth rate, hence, a plant with a high relative shoot growth rate such as maize acquired 6 times more K than spinach with only as much as half the relative growth rate of maize and one and half higher K concentration in its dry matter. In this study lower RGR_s could be the reason behind the efficiency of some species, for example, wheat and rye. However, lower RGR_s is not necessarily linked with high efficiency, since species like spinach and winter barley were not inefficient because of a high shoot demand for K on the roots (Table 3). Sadana and Claassen (1999) found that sugar beet with the highest relative shoot growth rate was more efficient than either wheat or maize. They concluded that sugar beet efficiency was not because of a low shoot demand on the roots, but because of a 4 times higher influx of the former as compared to the latter species. Hence, shoot growth rate alone can not explain the differences in K efficiency of the different plant species.

As explained above nutrient acquisition is either due to more roots per unit shoot, which enable the plants to take up more nutrients or the influx. Many authors associated increased nutrient uptake capacity with a larger root mass or root surface area, which results in a larger soil volume coverage and, hence, more efficient soil nutrient exploitation (Caradus and Snaydon, 1986; Cakmak et al., 1997). In this study, some plant species, for example, wheat and spring barley possessed high uptake efficiency due to a high root length-shoot weight ratio and low RGR_s (Table 3). Uptake efficiency of others, for example, elephant grass was mainly because of a low shoot demand on the roots and a very high influx.

Although all plant species grew with the same initial soil solution K concentration, some species, for example, sunflower were able to obtain a high influx, whereas others realised only one third of the former's influx (Table 5).

Ion diffusion to the roots is driven by the concentration gradient (Claassen and Steingrobe, 1999). Therefore, the higher the concentration difference (ΔC_L) between the bulk soil solution (C_{Li}) and the concentration at the root surface (C_{L0}) the higher is the concentration gradient and the flux from soil to roots. Sadana and Claassen (1999) attributed the higher K influx of sugar beet, as compared to wheat and maize, to the fact that sugar beet was able to decrease the C_{L0} to a much lower value than did the cereals. The theoretical C_{L0} values for some species were such that a diffusive flux to the roots, in the same order as the measured influx, was possible (Table 6). In such cases the efficiency mechanism could be a relatively larger root surface area as compared to K requirement and, consequently, a smaller influx. The results in table 6 show that for some plant species, for example, sunflower, elephant grass, sugar beet and oilseed rape, the concentration difference needed to derive the observed influx was higher than the initial K concentration of the soil solution. This resulted in calculated negative values of C_{L0}. However, this is not physically possible and could indicate that these species had developed mechanisms to release more K from the soil solid phase, for example, by solubilisation through root exudates. These findings support those reported by Claassen (1994).

All plant species were able to decrease the initial exchangeable K to different levels (Table 7). On the other hand, the soil solution K concentration except for some species, for example, wheat and maize cv. Ferris remained relatively unchanged or even increased. The soil solution K concentration of sugar beet, spinach and elephant grass was 6 times higher than the initial soil K concentration (Table 7). Similar results were found by Claassen (personal comm.) and Dieffenbach (1999). It does not seem possible that, at such high soil K concentrations, these plant species would not be able to achieve maximum growth. Meyer (1993) found that in nutrient solution, wheat, maize, sugar beet and oilseed rape achieved maximum yield at a K concentration of 25 µM, 75% of maximum yield at 5 µM and, after an adjustment phase, wheat and maize were able to grow with maximum growth rates at only 1µM K concentration. Also comparing the C_{Li} and the theoretical ΔC_L showed that some plant species were able to achieve a high K influx. A possible explanation is that the increased K in solution was not available to the plants, that is it was not actually in the soil solution, instead was due to the dispersion of very fine K containing soil particles into the solution which were also measured by the flame photometer and resulted in this high measured K concentration. The dispersion of the soil particles might have been caused by some type of root exudates of these plants. Pleßow (1998) using ultra-filtration membrane 1 kd, corresponding to a molecule circumference of 1 nm, to separate macromolecules and colloidal substances in seepage water, reported that up to 90% of the K was not found in the filtrate. It means this K was adsorbed and remained suspended in the solution.

On the other hand, inefficiency could have been caused by low root length-shoot weight ratio and/or high shoot growth rate, for example, oilseed rape and spinach, or extremely low uptake rate per unit root, for example, winter barley. These findings are in agreement with Föhse et al. (1988) who found that the studied plant species developed differing strategies for high P uptake efficiency. Whereas some had large root systems others had high uptake rate per unit of root length. Non of the species showed a combination of high values of both uptake components.

Conclusions

1. Different plant species had differing K efficiency under low K supply. Spring wheat was the most efficient because of a high root length-shoot weight ratio and low shoot growth rate, and spinach the least efficient species because of a low root length-shoot weight ratio and high shoot growth rate in addition to a low K influx.
2. Causes for high K efficiency were either low shoot growth rate and/or high root length-shoot weight ratio or a high uptake rate per unit root or influx.
3. Differences in influx among plant species may have been caused by differences in plant ability to decrease the K concentration at the root surfaces, thereby creating a larger concentration gradient needed for driving the observed flux by diffusion.
4. Some plant species even with high soil solution concentration were not able to obtain a high influx probably because the K was not actually in solution but on very fine soil particles dispersed in the soil solution. Root exudates may have enhanced this dispersion of soil particles.

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Chapter 3

Potassium Efficiency Mechanisms of Wheat, Barley and Sugar Beet Grown on a "K fixing" Soil Under Controlled Conditions

Abstract

Plant species differ in their K efficiency, but the mechanisms are not clearly documented and understood. Therefore, potassium efficiency of spring wheat, spring barley and sugar beet was studied, under controlled conditions, on a K fixing sandy clay loam. The effect of four K concentrations in soil solution ranging from low, 5 and 20 µM, to high, 2 and 10 mM, on plant growth and K uptake was investigated at 3 harvest dates (14, 21 and 31 days after sowing). The following parameters were determined: shoot dry matter (DM), root length (RL), root length-shoot weight ratio (RSR), shoot growth rate/root length (GR_s/RL), K uptake, K influx and soil solution K concentrations.

As compared to both cereals, sugar beet had a higher K concentration in dry matter, only one third or half the root length, one third to one sixth of RSR and 3-6 times higher GR_s/RL, which means the shoot of sugar beet had a 3-6 times higher K demand on the roots. Even at low K concentrations in soil, sugar beet had 7 to 10 times higher K influx than the cereals meaning a much higher K uptake efficiency. This shows that sugar beet was more effective in removing low available soil K.

Wheat and barley had a lower K concentration in dry matter at maximum yield. Their slow shoot growth and high RSR resulted in a low K demand on the roots.

At sub-optimal K concentrations, both cereals increased influx with age, an indication of adaptation to K deficiency. This might have been through increased physiological root activity, which might either be by improved uptake kinetics, or by root exudates that increase K solubility in soil. The mechanism of this adaptation merits closer investigation.

Model calculations were performed of the concentration differences (ΔC_L) between the bulk soil and the root surface needed to drive the measured influx. For cereals, the calculated ΔC_L was smaller than the concentration in solution, whereas for sugar beet, it was up to seven times higher. This indicates that sugar beet was able to mobilize K, but how this was achieved remains to be studied.

Introduction

Efficiency with regard to a specific mineral nutrient, is the ability of a species or cultivar to produce a high yield, in a soil limiting in this particular nutrient element for a standard species or cultivar. Several workers showed that plant species differ in their K efficiency (e.g. Zhang et al., 1999; Fageria et al., 2001). Plants may differ in their nutrient efficiency due to differences in efficiency in utilisation by the plant, or acquisition by the roots or both (Marschner, 1995). Efficiency in utilisation is defined as dry matter produced per unit K in the dry matter. Gardiner and Christensen (1990) and Trehan and Claassen (1998) reported different K efficiency between plant species due to differing utilisation efficiencies. Efficiency in acquisition is defined in terms of total uptake per plant or specific uptake per unit root length (Marschner, 1995). The uptake is a function of the morphological characteristics and/or physiological activity of the roots, which are the root system size and uptake rate per unit root and time or influx. Generally nutrient acquisition or uptake by roots is the most important factor in nutrient efficiency (Gutschick, 1993). Hence, differences in uptake may be caused by different influx due to differences in uptake kinetics such as the maximum influx theoretically achieved at infinite concentration (I_{max}), Michaelis constant (K_m) and minimum solution concentration at the root surface (C_{Lmin}) at which influx equals efflux, that is net influx (In) is equal to zero, or differences in root size often described by the root length shoot weight ratio (Claassen and Jungk, 1984; Föhse et al., 1988).

The objectives of this study were to investigate the K efficiency of wheat, barley and sugar beet and, furthermore, the reasons responsible for the differences in K efficiency of these plant species. To carry out these objectives, a pot experiment was conducted, under controlled conditions, on a low K soil "K fixing" soil in which four different soil solution K concentrations, were obtained by fertilisation. Three harvests were conducted in order to study the possible adaptations of the plant species to low K supply. First K efficiency of the crops was determined. In a second step root and shoot parameters were measured to evaluate their significance for differences in K efficiency. And in a third step model calculations were performed in order to evaluate whether plants possibly mobilized K chemically.

Materials and Methods

A pot experiment was conducted to study the K efficiency of spring wheat (*Triticum aestivum* L. cv. Star), spring barley (*Hordeum vulgare* L. cv. Madras) and sugar beet (*Beta vulgaris* L. cv. C+T). The plants were grown in a growth chamber with a day/night regime 16/8 hours, temperature of 25/18 °C and relative humidity 70 %. The photosynthetic active radiation during the day time was 250 µE m^{-2} s^{-1}.

Plastic pots of 3 L capacity were filled with 2.5 kg of Anglberg sandy clay loam soil from Bavaria, southern Germany, having pH ($CaCl_2$) 7.2, 33 % clay, 31 % silt and 3.8 % organic carbon. Four K levels 0, 0.6, 2.4 and 4.8 g kg^{-1} soil were added as KCl. These fertilisation levels resulted in a soil solution K concentration of 5 µM (K1), 20 µM (K2), 2000 µM (K3), and 10 mM (K4), respectively. Other nutrients added per kg soil were 200 mg N as NH_4NO_3, 50 mg Mg as $MgSO_4$ $.7H_2O$ and 200 mg P as $Ca(H_2PO_4)_2$. The plants were watered daily to a soil water content of 34% by weight. Three pots per treatment were left un-planted as control for soil solution concentration and exchangeable K determination. The treatments were replicated 3 times. Total number of plants grown for the first, second and third harvest, respectively, were 10, 5 and 5 for wheat and barley and 10, 3 and 3 for sugar beet. First harvest was 14, second harvest 24 and third harvest 31 days after sowing.

Shoots

At each harvest the plants were cut at the soil surface, after fresh weight determination, the dry weight was determined by drying the plants at 105°C till constant weight. The samples were then finely ground for chemical analysis.

Plant Chemical analysis

Sub-samples of the ground plant material were wet digested in a concentrated tri acid mixture (HNO_3, HC_LO_4, and H_2SO_4 in a volumetric ratio of 8:2:1, respectively). Potassium concentration was determined by flame photometry.

Roots

The roots in the whole pot were separated from the soil by washing them gently over a 0.2 mm sieve. The water remaining on the roots was removed by a 10 minutes centrifugation at 1200 rev. min^{-1}. After determining the root fresh weight, the root length was measured on representative sub-samples kept in 20% ethanol. The root length was measured using the method of Tennant (1975). A sub-sample of fresh root material (0.2-0.5 g depending on the plant species and age) were cut in small pieces and dispersed in water. The root length of the sub-sample was then determined in a plastic dish with grid lines 1.25 cm apart on its bottom. Counts of the intercepts of the roots with the vertical and horizontal lines were accumulated on a hand tally counter. Root length was calculated according to the equation:

$$\mathrm{RL} = \frac{11}{14} \times \mathrm{GD} \cdot \mathrm{N} \qquad [1]$$

where RL = Root length of the whole sample (cm)

GD = Distance between grid lines (1.25) (cm)

$\frac{11}{14}$ = Empirical factor

N = Number of intercepts

The sub-sample related to the total root fresh weight gives the total root length.

Relative shoot growth rate (RGR_s)

The relative shoot growth rate (RGR_s) was calculated using the following equation:

$$\mathrm{RGR_s} = \frac{\ln\left(\frac{\mathrm{SW_2}}{\mathrm{SW_1}}\right)}{t_2 - t_1} \qquad [2]$$

where:

SW = shoot dry weight (g)

t = time (s)

the indices 1 and 2 represent the first and second harvest.

Shoot growth rate in relation to root length (GR_s/RL)

This ratio is related to the K acquisition load on roots imposed by the shoot growth. It is calculated by dividing the shoot growth rate (GR_s) by the average root length (RL), assuming exponential root growth:

$$\frac{\mathrm{GR_s}}{\mathrm{RL}} = \frac{\mathrm{SW_2} - \mathrm{SW_1}}{t_2 - t_1} \times \frac{\ln\left(\frac{\mathrm{RL_2}}{\mathrm{RL_1}}\right)}{\mathrm{RL_2} - \mathrm{RL_1}} \qquad [3]$$

The net influx (In)

The influx is the net amount of a nutrient element which is taken up per unit root length or root surface area and unit time. A direct measurement of the influx is not possible, therefore, only an average influx can be calculated for a given time period. For calculating the influx, at least two harvests are needed in which the nutrient content and root length of the plants are known. Assuming that the roots of young plants have an exponential growth, the average influx is calculated after Williams (1948):

$$\mathrm{In} = \frac{U_2 - U_1}{t_2 - t_1} \times \frac{\ln\left(\frac{RL_2}{RL_1}\right)}{RL_2 - RL_1} \qquad [4]$$

where

U	=	nutrient element content in the plant	(mol)
RL	=	root length (or surface area)	(cm)
t	=	time	(s)

the indices 1 and 2 represent the first and second harvest.

Concentration difference between bulk soil and root surface (ΔC_L)

This is the difference in K concentration between bulk soil solution (C_{Li}) and concentration at the root surface (C_{Lo}) needed to drive a given flux by diffusion. This flux is given by the influx (In). The calculated ΔC_L was determined using the equation of (Barraclough, 1986):

$$\Delta C_L = \frac{\mathrm{In}}{4\pi D_L \Theta f}\left(1 - \frac{1}{1 - \pi r_0^2 RL_v} \ln \frac{1}{\pi r_0^2 RL_v}\right) \qquad [5]$$

where

D_L	=	K diffusion coefficient in water	($cm^2\ s^{-1} = 1.98 \times 10^{-5}$)
Θ	=	volumetric water content	($cm^3\ cm^{-3}$)
f	=	impedance factor calculated after Kaselowsky (1990)	
r_0	=	root radius	(cm)
RL_v	=	root length density	($cm\ cm^{-3}$)

Soil Analysis

Soil solution

The soil solution was obtained by a modified displacement technique of Adams (1974), whereby a 250 mL cylinder with a filter paper covering an opening at the bottom, was filled with moist soil. Using a peristaltic pump, water was allowed to drop slowly on the top, displacing the soil solution downwards, where it is taken in glass beakers. The displacement water was labelled with 4% KCNS in order to detect any contamination of the displaced soil solution by adding $FeCl_3$. The K concentrations were determined by flame photometry.

Exchangeable potassium and pH

One g field moist soil is weighed in a filter paper placed in a funnel. The soil was extracted 5 times with 10 mL 1 M NH_4OAc solution (pH 7) at 15 minutes intervals. The K concentration in the extract was determined by flame photometry. The soil K content was calculated on dry weight basis.

The pH was measured in 0.01 M $CaCl_2$ in a 1:2.5 soil:solution ratio. Soil samples were dried at 105^{o}C to constant weight and the gravimetric water content was determined.

Statistical Analysis

The data were statistically analysed using analysis of variance (ANOVA). Where significant differences were found, mean separation was conducted using the Tukey test.

Results

Relative and absolute dry matter yield

All species showed exponential growth pattern typical of young plants, regardless of the fertilisation level (Fig. 1). No fertilisation, at 5 µM K concentration in soil solution, dry matter yield for all plant species was reduced at all harvests, however, the reduction in yield depended on the plant species and age. Potassium efficient plants are those which are able at low K levels to produce a high proportion of maximum dry matter yield attainable at adequate K level. Accordingly at 5 µM, no differences existed in efficiency, since all species had more or less similar dry matter yield relative to yield under adequate K level (Table 1). At 20 µM level, however, wheat was the most efficient species with 77 % relative yield followed by barley 61 % and sugar beet 58 %.

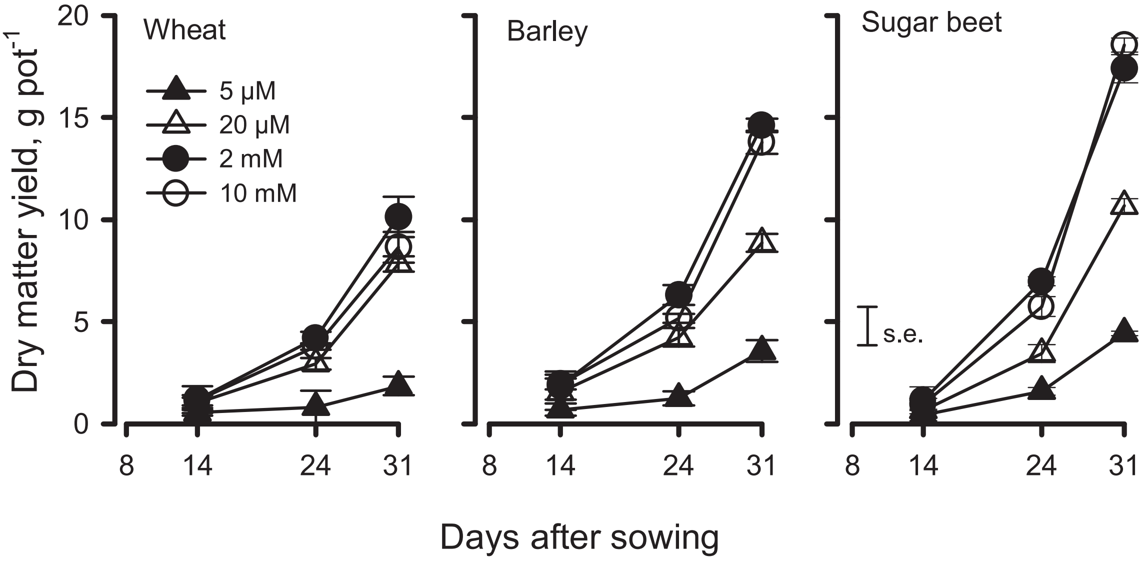

Fig. 1 *Dry matter yield of wheat, barley and sugar beet grown on a sandy clay loam at different soil solution K concentrations as a function of plant age.*

Table 1 *Relative dry matter yield (% of maximum yield) of wheat, barley and sugar beet grown on a sandy clay loam at different soil solution K concentrations at the 3 harvests*

Soil solution K conc.	Wheat	Barley	Sugar beet
µM	Relative yield, %		
5	22a*A$^{\infty}$	24 a A	24 a A
20	77 b A	61 b B	58 b B
2000	100 c A	100 c A	94 c A
10000	85 b A	94 c A B	100 c B
$^{\phi}$HSD	19.56	12.64	12.68

*Within a species values with different letters are significantly ($p \leq 0.05$) different from each other after Tukey. $^{\infty}$Between the species values followed by different capital letters are significantly ($p \leq 0.05$) different. $^{\phi}$Highest significant difference calculated after Tukey.

Potassium concentration in shoots

Potassium concentration in shoot dry matter is a measure for the nutritional status of the plant. To produce, for example, 90 % of maximum yield, plants require a certain K concentration in dry matter, which is the internal requirement. Plants with low internal K requirement have a high utilisation efficiency.

At low K concentrations, all species showed a similar K concentration in the shoots, only at the high K in soil, sugar beet had initially 2.0 % more K than wheat and barley. The K concentration in dry matter of all plant species increased significantly with increasing K concentrations in soil solution up to 2 mM (Fig. 2). It is interesting to note that at 5 µM, in contrast to all other K concentrations in soil solution, the K concentration in dry matter increased with time for all plant species from about 0.68 % to 1.0 % (Fig. 2).

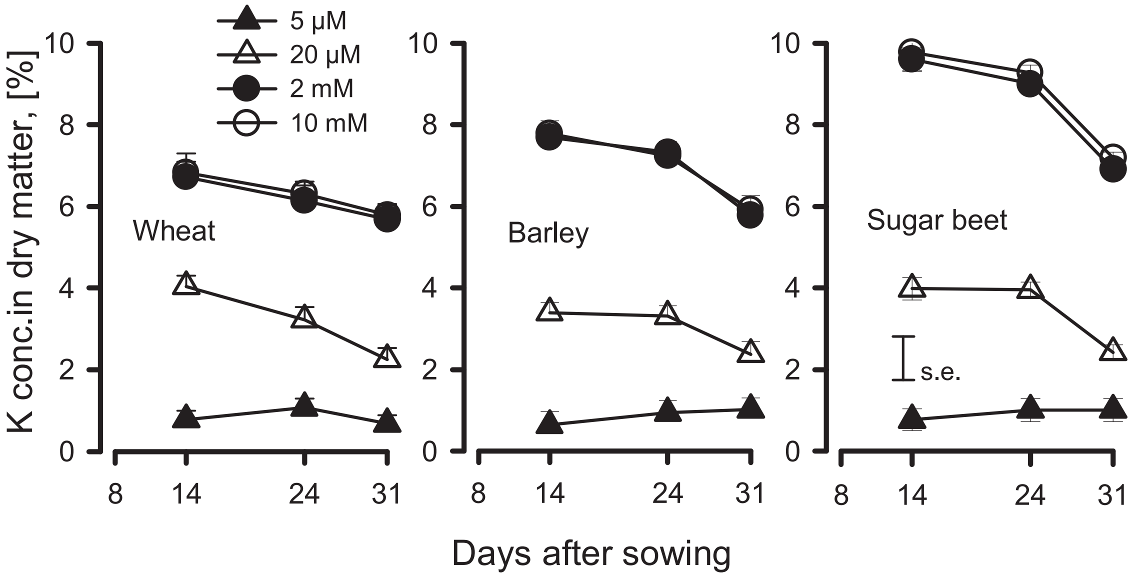

Fig. 2 *Potassium concentration in dry matter of wheat, barley and sugar beet grown on a sandy clay loam at different soil solution concentrations as a function of plant age.*

Relative shoot growth rate (RGR$_s$)

Fast growing shoots put a higher nutrient demand on the roots. For the cereals, differences in soil solution K concentration had an effect on RGR$_s$ at the early growth stages (Table 2). As for sugar beet soil solution K concentration had no significant effect on RGR$_s$ over the whole growth period.

Although no great differences were found for RGR$_s$ between the K treatments, the accuracy of the results should be regarded carefully, since RGR$_s$ is calculated from the difference between plants which differed in growing time and size. Accordingly there would be great fluctuations. Over the first growth period, sugar beet had 2 to 4 times higher RGR$_s$ as compared to wheat and barley, at the different K concentrations. Over the second growth period, sugar beet had between 1.6 to 1.2 higher RGR_s as compared to the cereals, at the different K concentrations (Table 2).

Table 2 *Relative shoot growth rate of wheat, barley and sugar beet grown on a sandy clay loam at different soil solution potassium concentrations at the first and second growth periods*

Time interval	Soil solution K concentration	Relative shoot growth rate		
		Wheat	Barley	Sugar beet
	µM	10^{-6} s^{-1}		
14-24	5	0.4 a*	0.6 a	1.6a
	20	1.1 b	1.1ab	1.9a
	2000	1.3 b	1.3 b	2.1a
	10000	1.3 b	1.0 ab	2.1a
	$^{\phi}$HSD	0.6	0.7	
24-31	5	1.4 a	1.5 a	1.7a
	20	1.4 a	1.1 a	1.9a
	2000	1.3 a	1.2 a	1.5a
	10000	1.2 a	1.4 a	1.9a

*Within a species and time interval values followed by different letters are significantly ($p \leq 0.05$) different from each other after Tukey.

$^{\phi}$ Highest significant difference calculated after Tukey.

Root length (RL) and root length shoot weight ratio (RSR)

As is shown in figure 1, sugar beet had similar or even higher absolute dry matter yield as compared to both cereals, at all K concentrations. However, the root length (Fig. 3) was only one third or half of that of the cereals. This resulted that throughout the growing period, and over all K concentrations, wheat had 3-6 times and barley 3-5 times higher RSR as compared to sugar beet (Fig. 4). It is interesting to note that for all species, the RSR was larger under K deficiency conditions. However, with increased growing time, the differences in RSR, between the soil solution K concentrations, increased for both cereals and decreased for sugar beet.

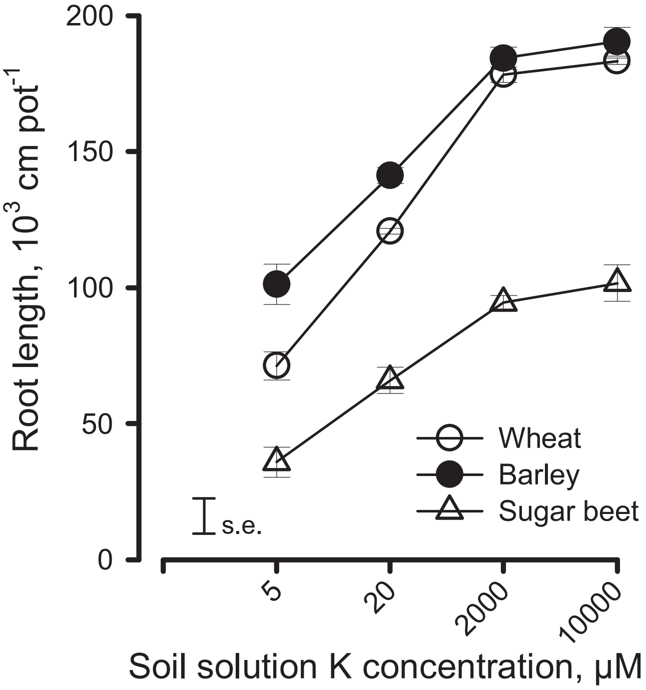

Fig. 3 *Root length of wheat, barley and sugar beet grown on a sandy clay loam at different K concentrations in the soil solution at the third harvest.*

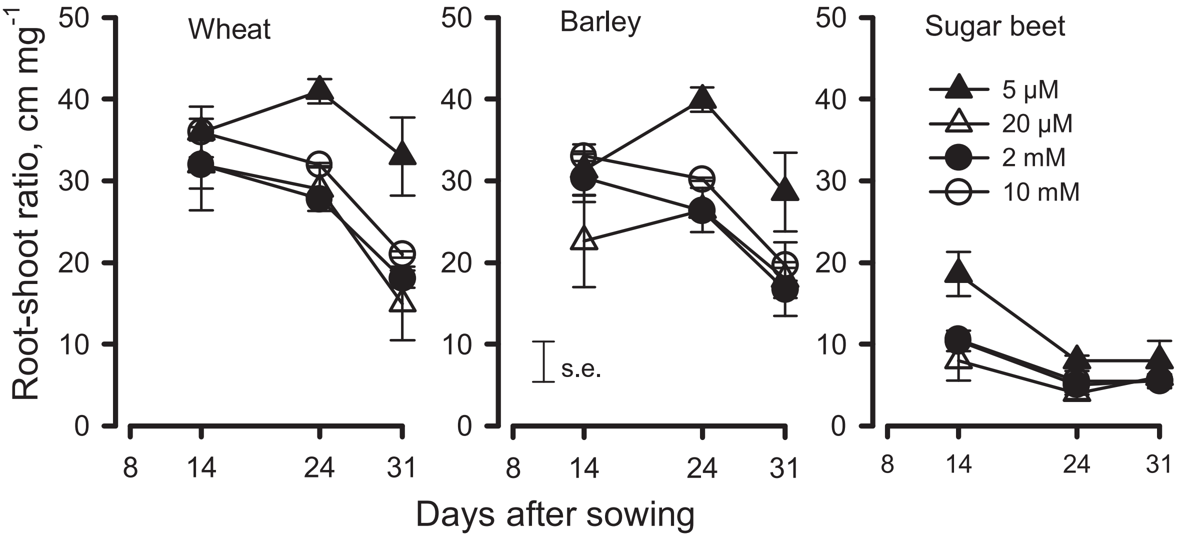

Fig. 4 *Root length-shoot weight ratio of wheat, barley and sugar beet grown on sandy clay loam at different K concentrations in the soil solution at the 3 harvests.*

Shoot growth rate to root length ratio (GR_s/RL)

Roots have to meet mainly the nutrient demand exerted by the new shoot growth. Hence, changes in root growth in response to nutrient deficiency are more adequately evaluated by the shoot growth rate to root length ratio (GR_s/RL). Figure 5 shows the shoot growth rate per unit of root length of wheat, barley and sugar beet at 2 mM K concentration in the soil solution, over the first and second growth periods. At this concentration, K was not limiting growth and the different species were growing optimally. This means the K uptake was not restricted (Table 3) and the plants could take up enough K to meet their requirement, which represents the K demand to be met by the roots. Sugar beet had significantly higher shoot growth rate per unit of root length as compared to both cereals, which were not significantly different from one another (Fig. 5). Hence, sugar beet had 3 to 6 times higher K demand on root as compared to wheat and barley. This indicates that sugar beet roots had higher uptake rates in order to meet the shoot demand.

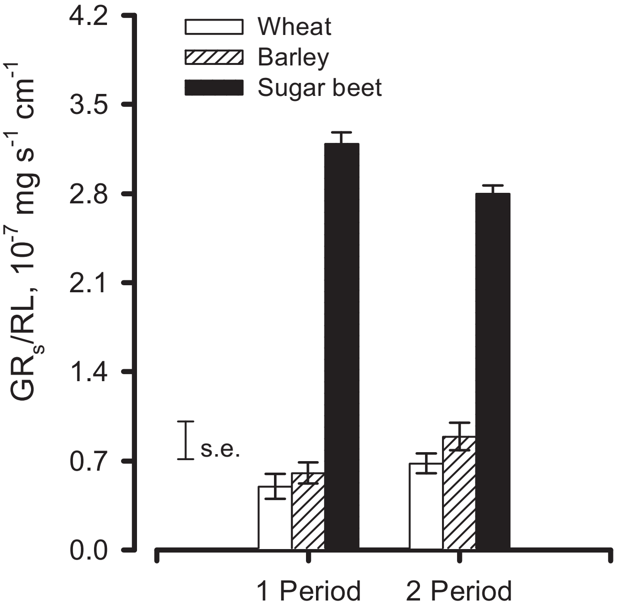

Fig. 5 *Shoot growth rate (GR_s) to root length (RL) ratio of wheat, barley and sugar beet at sufficient (2mM) soil solution concentration as a measure of shoot demand on the roots.*

Total K uptake and influx

Total K uptake is a measure for the ability of plants to acquire K from the soil and accumulate it in the shoots. It is the product of dry matter and the K concentration in dry matter. Figure 6 shows the total K uptake of wheat, barley and sugar beet, at the different K concentrations in the soil solution, at the third harvest. As compared to wheat, sugar beet total uptake was 3, 1.5, 2 and 3 times higher at 5 µM, 20 µM, 2 mM and 10 mM, respectively. The respective figures as compared to barley were 1.3, 1.2, 1.4 and 1.6 times higher uptake (Fig. 6).

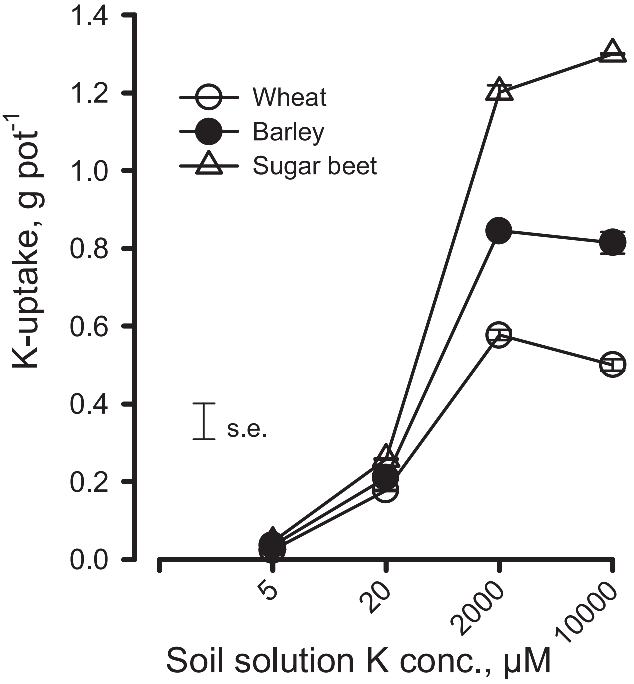

Fig. 6 *Potassium uptake of wheat, barley and sugar beet grown on a sandy clay loam at different K concentrations in the soil solution at the third harvest.*

The influx is a measure for the physiological activity of the roots. It gives the amount of K taken up per unit root and time. As could be seen from table 3 at the high K concentration of 2 mM, where the soil was not limiting K supply to the roots, sugar beet had in the respective first and second growth periods, 4 and 5 times higher influx as compared to both cereals because of a higher shoot demand on the roots. But also where soil was limiting K uptake (5 µM), sugar beet was able to obtain 4 to 10 times higher influx as compared to wheat and barley.

At the sub-optimal K concentration of 5 µM, all species obtained a higher influx at the second as compared to the first growth period. The same also happened for the cereals at 20 µM. This indicates that the plants were able to adapt to low K supply by increasing their root physiological activity.

Table 3 *Potassium influx (In) of wheat, barley and sugar beet at different soil solution K concentrations (C_{Li}) at the first and second growth periods*

	First growth period		Second growth period	
	C_{Li}	In* $^{\psi}$	C_{Li}	In
	µmol	mol 10^{-14} cm^{-1} s^{-1}	µmol	mol 10^{-14} cm^{-1} s^{-1}
Wheat	5.0	0.50 a (0.01)*	4.6	1.27 a (0.06)
	20.8	2.89 b (0.32)	17.0	3.40 a (0.42)
	2617.0	9.37 c (1.01)	2070.0	7.88 b (1.62)
Barley	5.0	0.70 a (0.30)	4.7	1.53 a (0.15)
	18.9	3.76 a (1.24)	16.8	4.39 a (0.32)
	2410.0	11.0 b (1.70)	1720.0	9.75 b (1.45)
Sugar beet	4.5	5.05 a (0.38)	3.7	3.74 a (1.32)
	22.8	36.5 ab (5.75)	21.6	16.40 a (2.36)
	2632.0	77.40 b (3.09)	1470.0	58.9 b (10.8)

*Within a species and growth period values followed by different letters are significantly ($p \leq 0.05$) different from each other after Tukey. Values between brackets represent the standard error of means.

Discussion

The ability of different plant species as well as genotypes within a species to grow with differing efficiencies, at sub-optimal K levels, is reported for plants grown in soils (Fageria et al., 2001), and for plants grown in nutrient solution cultures (Meyer, 1993; Trehan and Claassen, 1998). This indicates that besides K concentration levels in the rooting medium, plant development and K uptake depend also on plant characteristics. The objective of this study was to investigate the reasons behind differing K efficiency of wheat, barley and sugar beet.

From an agronomic point of view the efficiency criteria are the differences in relative yield of the plants grown under deficient K concentrations (Marschner, 1995). As is presented in table 1, at 5 µM K concentration, differences in K efficiency were not found between the plant species. At 20 µM level, wheat proved to have a higher efficiency reflected in a relative yield of 77 %, as compared to barley (61 %) and sugar beet (58 %). This means that at a soil solution concentration of 5 µM, not only plant growth was extremely affected, but presumably also the metabolism was disturbed. However, at 20 µM soil solution K, it was possible to observe the differences in plant species performance at sub-optimal K concentrations.

Genotypical differences in nutrient efficiency could be due to differences related to uptake, transport and utilisation within plants (Marschner, 1995). As defined in the introduction, utilisation efficiency refers to the dry matter production per unit nutrient in the dry matter. At 20 µM K concentration, all species accumulated between 2 and 4 % K in dry matter (Fig. 2). The total concentrations of nutrients can be a result of dilution and concentration effects, but if we consider how the relative yield relates to K concentrations in dry matter, we find that wheat, which produced almost 80 % (Table 1) of its maximum yield with 2.4 % K concentration in dry matter (Fig. 3), was the species with the highest utilization efficiency. At maximum yield barley had 6 to 8 %, whereas sugar beet had 7 to 9 % K. This indicates that sugar beet had the least utilisation efficiency of the 3 species studied.

Values given by Bergmann (1993) for K concentration in dry matter required for optimum dry matter yield are 3.5-6.0 % for sugar beet and 2.9-3.9 % for wheat. Our results show much higher K concentrations in dry matter for optimum yield, which are in agreement with those of Trehan and Claassen (1998) who found that in solution culture, wheat and sugar beet needed 6 % for producing 90 % of maximum yield. The K concentrations in dry matter for optimum yield given by Bergmann (1993), were measured at much advanced plant growth stages, for example, at shoot elongation by wheat and full-expanded leaf by sugar beet. Also the optimum yield represents the economic yield produced by the plants, whereas in this study, dry matter yields represent only shoot yield. Also the plants were relatively young (31 days old) where the highest K concentration, especially by K deficient plants, is found in young intensively growing plant parts, which have a high K requirement because of its active metabolism Koch and Estes (1976). Moreover, from our data we can not exactly specify a certain K concentration by which 90 % relative yield was produced. If we consider the relative yields (Table 1) and the K concentration in dry matter (Fig. 3) we find, for example, that sugar beet produced at a K concentration in dry matter below 3.5 %, only 54 % of optimum yield. On the other hand, above 6 % K concentration in dry matter, more than 90 % of its optimum yield was produced.

One of the uptake components is the size of the root system. Several authors linked uptake efficiency with larger root systems (Dong et al., 1995; Snapp et al., 1995). In this study, the root shoot ratio (RSR) is used as a measure for the size of the root system in relation to the shoot. From the results, it is seen that regardless of the K concentration in soil solution, wheat and barley had 3 to 6 times larger RSR as compared to sugar beet (Fig. 4). As could also be seen that generally for all plant species RSR was higher at sub-optimal K concentration of 5 µM as compared to the optimal concentration of 2 mM. This does not mean that the plants increase the absolute root size at deficient K concentrations as a mechanism to increase uptake, but because K deficiency sharply decreased the shoot development and, consequently, influenced the RSR. The differences in RSR between the K concentrations, which increased with time for the cereals but decreased for sugar beet, could indicate that compared to the cereals, sugar beet had a higher ability to adjust to the K deficiency conditions. These results disagree partially with the findings of Trehan and Claassen (1998) who reported somewhat increased root growth at low K concentrations for wheat and sugar beet, but for potato the root-shoot ratio was reduced to one half. Apparently plant species react differently to low K supply.

Further differences between the species were found also in the relative shoot growth rates. Sugar beet had much faster growing shoots (1.2 to 4 times higher RGR_s) as compared to both cereals, at all K concentrations, over the whole growth period (Table 2). At 2 mM K concentration, K was not limiting growth and the plants grew optimally. The higher RGR_s and small root system of sugar beet and the fact that the K concentrations needed for optimum growth, were as high or higher than for the cereals (Fig. 2), resulted in 3 to 6 times higher shoot growth per unit root, imposing a higher demand on the roots for K acquisition as compared to wheat and barley (Fig. 5). This shows that sugar beet had the combined disadvantage of a low utilisation efficiency and a very high shoot growth rate per unit of root. In contrast, a further contribution to K efficiency of wheat is the low rate of shoot growth, which means a lower demand on the roots for nutrient acquisition.

Regarding the total uptake as a measure for the plant K acquisition efficiency, however, shows that sugar beet, which had 2 to 3 and 1.2 to 1.6 times higher uptake as compared to wheat and barley, respectively, as the species with the highest uptake efficiency (Fig. 6). This higher uptake efficiency of sugar beet can only be explained by a very high uptake rate per unit root and unit time or influx, which is the second component of the uptake efficiency. Under the high K concentration of 2 mM, the soil was not limiting in K and all plant species could take up K without constraints. Here we found that sugar beet obtained an influx 5 times higher than that of the cereals (Table 3). Nevertheless, it is much more important to consider the influx at soil solutions limiting in K supply such as the 5 and 20 µM K concentrations. As was shown in the results, even when the soil was deficient in K at 5 µM, sugar beet was able to obtain 7 to 10 times higher influx than wheat and barley. Moreover, at 5 µM, sugar beet had almost double the influx of both cereals at the 4 times higher K concentration of 20 µM (Table 3). What are the possible reasons which enabled sugar beet even at very low K concentration in soil solution to obtain a higher influx than both cereals? Could it be that sugar beet increased its root physiological capabilities by changing the uptake kinetics? Meyer (1993) found such an adaptation by young wheat and maize plants, and suggested changing uptake kinetic parameters as a possible mechanism. The author reported increased maximum influx (I_{max}) values by both species when grown at low K concentration, and found a decrease in K_m value and as a result increase in K efficiency with plant age. He concluded that changing the physiological activity of the roots was the reason for the increase in K efficiency with age of plants grown in solution culture. Also our results show that both wheat and barley had higher influx at deficient K concentrations, in the second as compared to the first growth period. The reason for the higher influx in the latter period could possibly be explained by changes in the physiological activity of the roots. This means the plants might have been able to adapt to the low K concentrations by adjusting the uptake kinetics of their roots over the growth period. If such a physiological adaptation to low K concentrations in soil solution was possible, then the fact that the influx at 5 µM was much lower than that at 20 µM at both growth periods, could mean that K transport in soil limited uptake.

In order to assess the limitation of K uptake by soil transport the model of Barraclough (1986) was used. The model calculates the theoretical difference in K concentration (ΔC_L) between bulk soil solution (C_{Li}) and concentration at the root surface (C_{L0}), necessary to drive the diffusive flux to the roots of the plants. The higher the influx the greater must be the diffusive flux to the roots and, consequently, the greater is the needed ΔC_L.

As is seen from table 3, at the high K concentration in soil solution (2650 µM), uptake was not limited by K transport to the roots, since the concentration difference (ΔC_L) needed to drive the flux by diffusion ranged only between 20 µM for cereals and 300 µM for sugar beet. At the low K concentration of 5 µM, in the first growing period, for cereals the calculated ΔC_L, necessary to drive the measured influx was smaller than C_{Li}. This indicates that the plants were not able to create a maximum diffusive flux to the roots. However, at the second growth period, the calculated ΔC_L came close to the concentration of 5 µM in the bulk soil, creating almost the maximum concentration gradient. Perhaps at the early stage of growth, the plants did not adjust I_{max} or had a high C_{lmin} value. The ability of the plants to achieve a maximum ΔC_L, in the second growth period, could indicate that the plants, allowing for a stronger concentration decrease at the root surface, have undergone an adjustment in their uptake kinetics.

Table 4 *Soil solution K concentration (C_{Li}), concentration difference between bulk soil and root surface (ΔC_L) as calculated after (Barraclough, 1986) at the two growth periods at three K levels for wheat, barley and sugar beet*

Wheat				Barley				Sugar beet			
Growth period											
First		Second		First		Second		First		Second	
C_{Li}	ΔC_L	C_{Li}	ΔC_L	C_{Li}	ΔC_L	C_{Li}	ΔC_L	C_{Li}	ΔC_L	C_{Li}	ΔC_L
µmol L^{-1}											
5.03	1.87	4.56	4.20	5.03	2.28	4.68	4.03	4.51	24.4	3.72	14.67
20.80	8.32	17.00	9.08	18.90	10.71	16.80	10.65	22.78	158.62	21.6	57.74
2617	27.50	2070	19.47	2410	28.90	1720	23.02	2632	298.75	1470	182.45

As for sugar beet, the calculated ΔC_L was up to 7 times higher than the C_{Li}, i.e. transport to the roots was higher than actually possible by diffusion at the given K concentration in soil solution. There are usually large amounts of total K in the soil, but its available fraction and concentration in the soil solution is not always sufficient to cover plant needs (Rengel, 1999). Apparently sugar beet was able to mobilize these reserves. Since K transport was limiting, a further change in the root uptake kinetics would not help for increasing uptake, since the highest possible diffusive flux to the roots and maximum ΔC_L were already established. Moreover, the results of Trehan and Claassen (1998) showed that for plants adapted to low K conditions, the uptake physiology of wheat and sugar beet were more or less similar. This leads to the conclusion that the higher measured influx of sugar beet was not or not only due to an increased uptake kinetics, but to an increased K availability in the rhizosphere of sugar beet.

This could indicate that sugar beet had developed mechanisms to release more K from the soil solid phase, for example, by solubilisation through root exudates. Chemical mobilisation of mineral nutrients in the rhizosphere by plant roots is reported to have a significant role in the phosphate and micro-nutrients nutrition of plants (Marschner et al., 1986; Gerke et al., 1994; Rengel et al., 1998). Little information exists about K mobilisation. Hence, to try to find out the responsible mechanisms behind the K efficiency of sugar beet, simulating the K uptake by these plant species using an uptake simulation model is conducted, and the results will be discussed in a separate chapter.

Conclusions

1. Plant development and K uptake is determined not only by the K concentration in soil solution but also by plant characteristics.
2. From an agronomic point of view, at 60 to 80 % of maximum yield, wheat had the highest K utilisation efficiency followed by barley and sugar beet. To achieve maximum yield sugar beet had a higher concentration than the cereals.
3. Both wheat and barley had a low internal K requirement and a low demand for K acquisition on the roots because of a high root-shoot ratio and a low shoot growth rate. On the other hand, sugar beet had both a high internal K requirement and shoot demand for K acquisition on the roots due to a low root-shoot ratio and a high shoot growth rate.

4. Even though sugar beet had a high shoot demand for K acquisition by the roots, it proved to have a very high uptake efficiency, where at limiting soil K, its influx was 7 to 10 times higher than that of wheat and barley.
5. This influx was much higher than the transport capacity of the soil. It remains an important question to find out the mechanisms enabling sugar beet to realise such a high influx.

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Chapter 4

Potassium Efficiency of Wheat and Sugar Beet Evaluated Under Field Conditions

Abstract

In a pot experiment under controlled conditions, sugar beet proved to have a very high uptake efficiency Nutrient supply to plants growing in the field is influenced by uncertainties, related to nutrient loss and its dependence on biophysical factors, which affect the root morphology and physiology, thereby directly affecting nutrient uptake efficiency. Hence, this study was conducted to investigate the K efficiency of wheat and sugar beet under field conditions, and to identify the varying mechanisms or factors behind their efficiency.

In the field data were obtained from a long term fertiliser experiment, on a K "fixing" sandy clay loam in Bavaria, southern Germany, in which K fertilisation rates had varied from 0 to 1000 kg K ha^{-1} year^{-1} with the last K application in 1986. In 1997, sugar beet and spring wheat were sown on March 13th and April 4th, respectively. At each of 4 and 5 harvests for wheat and sugar beet, respectively, random samples of shoots, roots and soil of each species were analysed from the unfertilised (-K) and the highest fertiliser level of 1000 kg K ha^{-1} (+K) treatments.

Sugar beet and wheat had similar K efficiency producing 76 % and 80 % beet and grain yield, respectively on unfertilised relative to fertilised treatments. As compared to wheat, sugar beet had a higher internal requirement, 2 times higher shoot growth rate (GR_s), 34 to 48 % of the wheat root length (RL), consequently a larger GR_s/RL, that is higher demand for K uptake on the roots. However, it showed an exceptionally high uptake efficiency of the single roots or influx, which was 5 times higher on unfertilised treatments, as compared to wheat. Wheat K efficiency was attributed to a higher utilisation efficiency or lower internal requirement, slow growing shoots and a large root system.

Further investigations are necessary to study mechanism by which sugar beet was able to achieve a higher influx than wheat.

Introduction

Nutrient element efficient plant species are those which grow and yield well on soils of low fertility as compared to inefficient species (Petterson and Jensen, 1983; Graham and Rengel, 1993; Gouerly et al., 1994). Plant species and even genotypes within a species differ in their K efficiency (Jianjun and Gabelman, 1995). According to Sauerbeck and Helal (1990) defining nutrient efficiency as plant yield per unit of nutrient supply, means its dependency on two interrelated groups of plant factors. These are: a) plant properties related to the uptake efficiency, which is nutrient uptake relative to its supply, b) factors related to utilisation efficiency, representing plant yield relative to nutrient uptake. Plant factors related to the uptake efficiency are: a) morphological root characteristics such as root system size and root hairs. A large root system to satisfy shoot nutrient requirement is beneficial for nutrient efficiency, as it means less nutrient uptake effort per unit root and allows for exploitation of a larger soil volume for nutrients (Steingrobe and Claassen, 2000). Higher root length-shoot weight ratios are reported under deficiency of different macro and micro nutrients (Steingrobe and Schenk, 1991; Cakmak et al., 1997; Jungk and Claassen, 1997). The other uptake efficiency component is root physiological activity such as different uptake kinetics, which result in different uptake rates per unit root and time or influx (Steingrobe and Claassen, 2000), and ability to chemically change the rhizosphere to improve the availability of nutrients (Sattelmacher et al., 1994).

Wheat (*Triticum aestivum* L.) would be expected to be K efficient because of a large root system (Claassen, 1994; Steingrobe and Claassen, 2000) and low K internal requirement (2.9-3.9 %) for maximum yield (Bergmann, 1993). Sugar beet (*Beta vulgaris* L.), on the other hand, has a much smaller root system and higher (3.5-6.0 %) internal K requirement (Bergmann, 1993), nevertheless, as is seen in the last chapter, in a pot experiment, sugar beet proved to have an extremely high uptake efficiency.

The objectives of this study were:

1- To investigate the K efficiency of wheat and sugar beet under field conditions on a low K supplying (K fixing) soil.

2- To identify mechanisms and factors responsible for differences in K efficiency of wheat and sugar beet.

To study these objectives wheat and sugar beet were grown in the field on a long term K fertiliser experiment on a K-"fixing" soil of low K supply, in 1997, in Bavaria southern Germany. Four to five harvests were performed during the growing season in order to evaluate shoot and root growth and K uptake. At each harvest, K in soil solution and exchangeable K were determined in order to relate K uptake to K in soil.

Materials and Methods:

The field experiment was conducted in Bavaria in southern Germany (Anglberg), on a sandy clay loam with a high K fixing ability having 33 % clay, 31 % silt, 3.8 % C_{org} and pH ($CaCl_2$ 0.01M) 7.2. The study was conducted on the site of a long term fertiliser experiment which started in 1976 and ended in 1986, thereafter all plots received no K fertiliser. The plants studied were from the unfertilised treatments (NH_4-OAc exchangeable K (K_{exch}.) 782 µmol K kg^{-1} soil, soil solution concentration (C_{Li}) 4.2 µM), and from the highest fertiliser level of 1000 kg K ha^{-1} a^{-1} (K_{exch}.1047 µmol K kg^{-1} soil , C_{Li} 7.5 µM). The soil analysis values given here were obtained 6 months before the conduction of the experiment. In 1997, spring wheat cv. Star, and sugar beet cv. Kawetina were sown on 50 m^2 plots on March 13th and April 04th, respectively. Before sowing 43 kg P and 80 kg N ha^{-1} were applied to the soil in form of super-phosphate and ammonium sulphate and ammonium nitrate, respectively. Harvests were carried out on 27th May, 24th June, 08th July, 05th August for both crops and on 07th October for sugar beet. At each harvest date, 3 sub-samples of plants, roots and soil were taken from random areas of each plot.

Shoots:

Every sample for wheat was harvested from an area of 0.5 m^2, final harvest 1 m^2, per treatment. The plants were separated into straw and ears after flowering. Samples from an area of 1.5 m^2 were harvested for sugar beet and the plant analysis was carried out on the leaves and the beets separately. After fresh weight determination, the dry weight was determined by drying representative samples at 105°C till constant weight. The samples were then finely ground for chemical analysis.

Chemical analysis of plant material:

Sub-samples of the ground plant material were wet digested in a concentrated tri acid mixture (HNO_3, $HClO_4$, and H_2SO_4 in a volumetric ratio of 8:2:1, respectively). Potassium concentration was determined by flame photometry.

Root sampling and samples preparation

Roots were sampled from the same plots as the shoot samples using a hand auger with 8 cm diameter Böhm (1979). The sampling was carried out in the 0-15, 15-30, 30-60 cm soil layers. The 60-90 cm layer was sampled only at the final harvest, since it generally contains few roots and the soil solution K concentration was very low and as such did not contribute much to plants K nutrition.

The samples consisted of a mixture of 2 soil cores, 1 in and 1 between the rows of wheat and 4 soil cores in and between the row for sugar beet. The cores were soaked in water overnight and the roots washed out carefully over a 0.2 mm sieve. The water remaining on the roots was removed by a 10 minute centrifugation at 1200 rev. min^{-1}. After determining the root fresh weight, the root length was measured on representative sub-samples. The sub-samples of wheat were kept in a 20 % ethanol solution and those of sugar beet in a 20 % ethanol and 0.01 mM citric acid mixture at 4 ^{o}C. The root length was measured using a line intersection method Tennant (1975). A sub-sample of fresh root material were cut in small pieces and dispersed in water. The root length of the sub-sample was then determined in a plastic dish with grid lines 1.25 cm apart on its bottom. Counts of the intercepts of the roots with the vertical and horizontal lines were accumulated on a hand tally counter. Root length was calculated according to the equation:

$$\mathrm{RL} = \frac{11}{14} \times \mathrm{GD} \cdot \mathrm{N} \qquad [1]$$

where

RL = Root length of the whole sample (cm)

GD = Distance between grid lines (1.25) (cm)

$\frac{11}{14}$ = Empirical factor

N = Number of intercepts

The sub-sample related to the total root fresh weight gives the total root length.

Shoot growth rate (GR_s)

The shoot growth rate was calculated using the following equation:

$$GR_s = \frac{SW_2 - SW_1}{t_2 - t_1} \qquad [2]$$

where:

SW = shoot dry weight (g)
t = time (s)

the indices 1 and 2 represent the first and second harvest.

Shoot growth rate in relation to root length (GR_s/RL)

This ratio is related to the K acquisition load on roots imposed by the shoot growth. It is calculated by dividing the shoot growth rate (GR_s) by the average root length (RL):

$$\frac{GR_s}{RL} = \frac{SW_2 - SW_1}{t_2 - t_1} \times \frac{2}{RL_1 + RL_2} \qquad [3]$$

the indices 1 and 2 represent the first and second harvest.

Influx (In)

The influx is the net amount of a nutrient element taken up per unit root length or root surface area and time. A direct measurement of the influx is not possible, therefore, only an average influx can be calculated for a given time period.

For calculating the influx, at least two harvests are needed in which the nutrient content and root length of the plants are known. Assuming linear root growth by plants growing in the field, the influx was calculated as:

$$In = \frac{U_2 - U_1}{t_2 - t_1} \times \frac{2}{RL_1 + RL_2} \qquad [4]$$

where

U = nutrient element content in the shoot (mol)
RL = root length (cm)
t = time (s)

the indices 1 and 2 represent the first and second harvest.

Soil Analysis

Soil solution

The soil solution was obtained by a modified displacement technique of Adams (1974), whereby a 250 mL cylinder with a filter paper covering an opening at the bottom, was filled with moist soil collected from the field. Using a peristaltic pump, water was allowed to drop slowly on the top, displacing the soil solution downwards, where it is collected in acid-washed glass beakers. The displacement water was labelled with 4% KCNS in order to detect any contamination of the displaced soil solution by adding $FeCl_3$. The K concentrations were determined by flame photometry.

Exchangeable potassium, pH and water content

One g field moist soil is weighed in a filter paper placed in a funnel. The soil was extracted 5 times with 10 mL 1 M NH_4OAc solution (pH 7) at 15 minutes intervals. The K concentration in the extraction solution was determined by flame photometry. The soil K content was calculated on dry weight basis.

The pH was measured in 0.01 M $CaCl_2$ in a 1:2.5 soil:solution ratio. Soil samples were dried at 105^{o}C to constant weight and the gravimetric water content was determined.

Statistical Analysis

The data were statistically analysed using analysis of variance (ANOVA), where significant differences were found, mean separation was conducted using the Tukey test.

Results

Exchangeable K (K exch.) and soil solution K concentration

The mean values of exchangeable potassium, over the whole growth period and soil depths under sugar beet, were 973 and 670 µmol kg^{-1} soil with and without fertilisation, respectively. The respective values under wheat, were 803 and 625 µmol kg^{-1} soil. The exchangeable K decreased with increasing soil depth under both crops (Appendix Table 1). Generally the soil solution concentration decreased with increasing soil depth. Under both crops, soil solution was relatively low and was lower under wheat than sugar beet (Appendix Table 2).

Relative and absolute dry matter yield

Figure 1 shows the dry matter yield of wheat leaves and straw and sugar beet leaves with (+K) and without (-K) fertilisation at the different harvests. Except for May, fertilisation increased the dry matter yield of wheat leaves or straw significantly ($p \leq 0.05$). On the other hand, no significant differences were detected for grains dry matter yield between fertilised and unfertilised treatments (Fig. 1). Over the whole growth period, there were no significant differences between dry matter yield of sugar beet leaves on fertilised and unfertilised plots. However, in August and October leaf weight of the unfertilised treatments tended to be higher than that on the fertilised ones (Fig. 1). Beet dry matter yield though, was increased significantly ($p \leq 0.05$) by K fertilisation (Fig. 1). The dry matter yield of grains and beet of unfertilised relative to fertilised treatments did not differ greatly between species corresponding, to 81 % for wheat and 76 % for sugar beet.

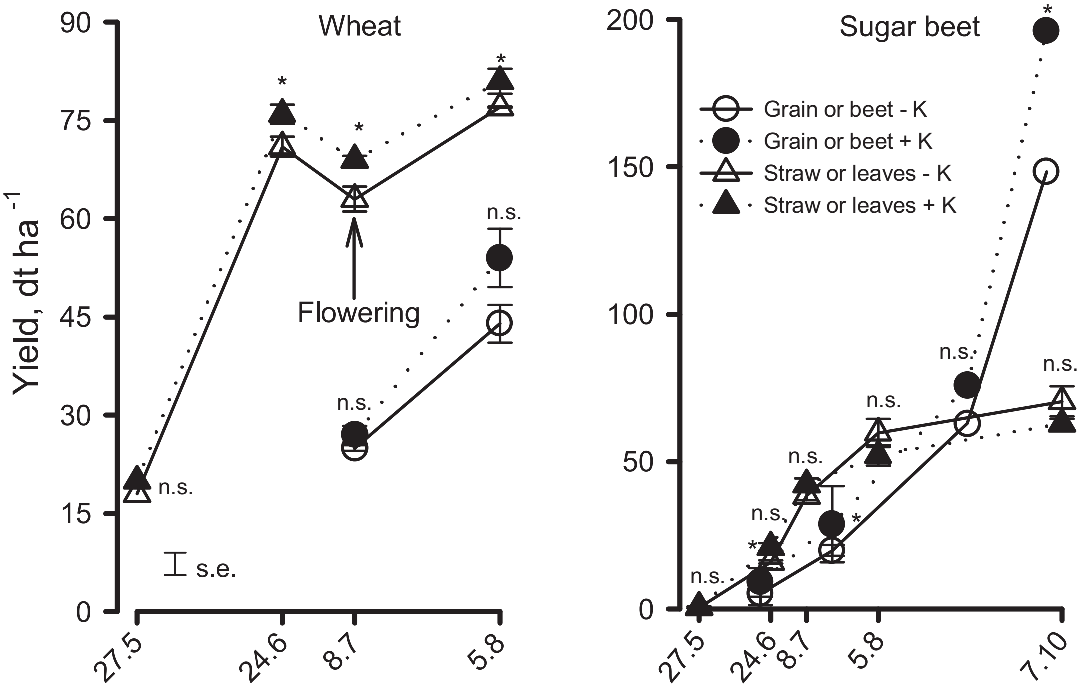


Fig. 1: *Dry matter yield of spring wheat (leaves and straw + grains) and sugar beet (leaves + beet) grown on a sandy clay loam in the field with (+ K) and without (- K) K fertilisation. n.s. no significant difference ($p < 0.05$) between (+K) and (-K) treatments.*
** significant differences ($p < 0.05$) between (+K) and (-K) treatments.*

Potassium concentration in shoots

To assess the nutritional status of the plants, K concentration in dry matter was measured (Fig. 2). Potassium concentration in dry matter of wheat shoot ranged between 3.79 to 2.07 % on fertilised, and 2.96 to 1.42 % on unfertilised treatments. The respective values for sugar beet leaves were 6.55 to 3.46 % and 5.28 to 2.05 %. As is seen, both crops had deficient K levels on unfertilised treatments. The effect of K fertilisation was significant ($p \leq 0.05$) for both crops. The K concentration in grains started in July with 1 % and decreased to around 0.5 % at final harvest. Differences between (+K) and (-K) were small, but at final harvest significant with a tendency of the (+K) to show a lower K concentration. Potassium concentration of beets started in June with about 2.7 % and decreased to about 0.5 % at final harvest. The (+K) plot always showed significantly higher K concentration (Fig. 2).

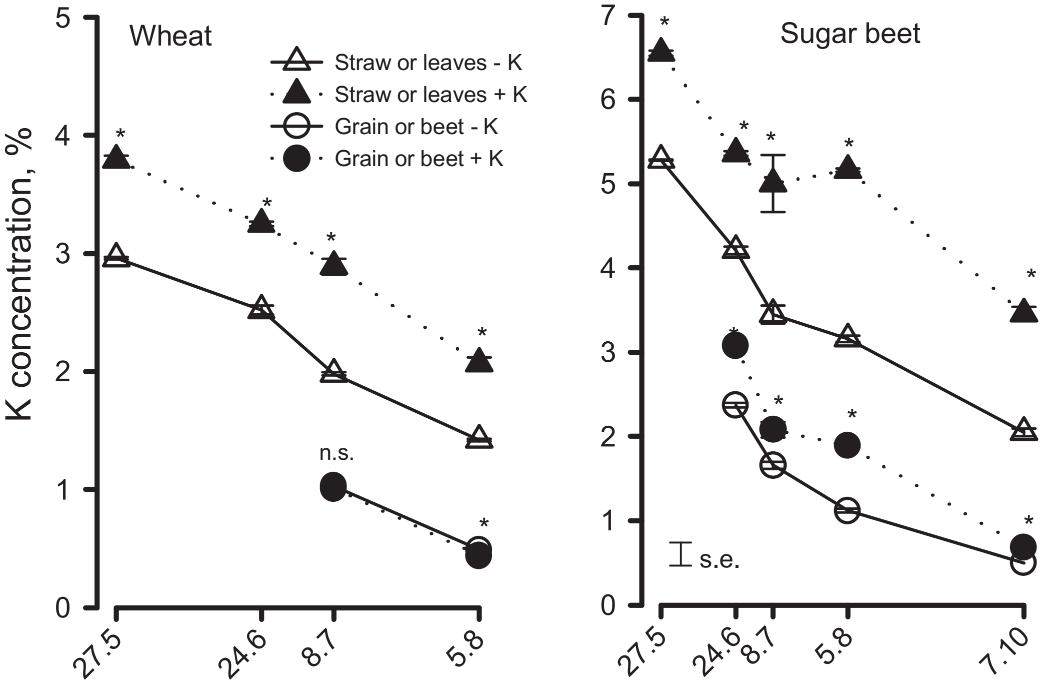


Fig. 2 *Potassium concentration in dry matter of spring wheat (shoot + grain) and sugar beet (leaves + beet) grown on a sandy clay loam in the field with (+ K) and without (- K) K fertilisation. n.s. no significant difference ($p < 0.05$) between (+K) and (-K) treatments.*
* *significant differences ($p < 0.05$) between (+K) and (-K) treatments.*

Shoot growth rate (GR_s)

Figure 3 shows the GR_s of wheat and sugar beet with (+K) and without (-K) fertilisation over the different growth periods. Except for the growth period 27.5-24.6, sugar beet had 2 times higher shoot growth rate than wheat, in the growth periods 24.6-8.7 and 8.7-5.8. Wheat had generally lower, though statistically not significant GR_s on unfertilised as compared to fertilised treatments. The effect of K was largest on the GR_s of sugar beet late in the season due to beet growth.

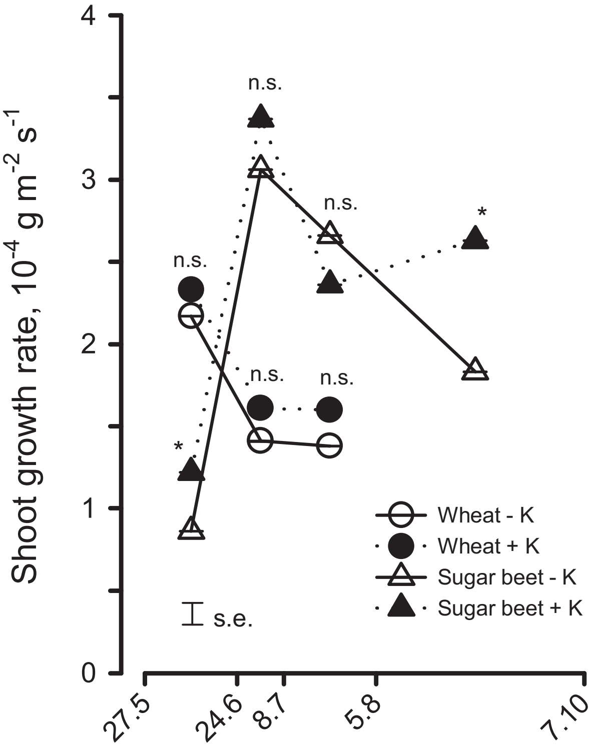


Fig. 3: *Shoot growth rate of spring wheat (shoot + grains) and sugar beet (leaves + beet) at different growth stages on a sandy clay loam in the field with (+K) and without (-K) K fertilisation. n.s. no significant difference (p< 0.05) between (+K) and (-K) treatments. * significant differences (p< 0.05) between (+K) and (-K) treatments.*

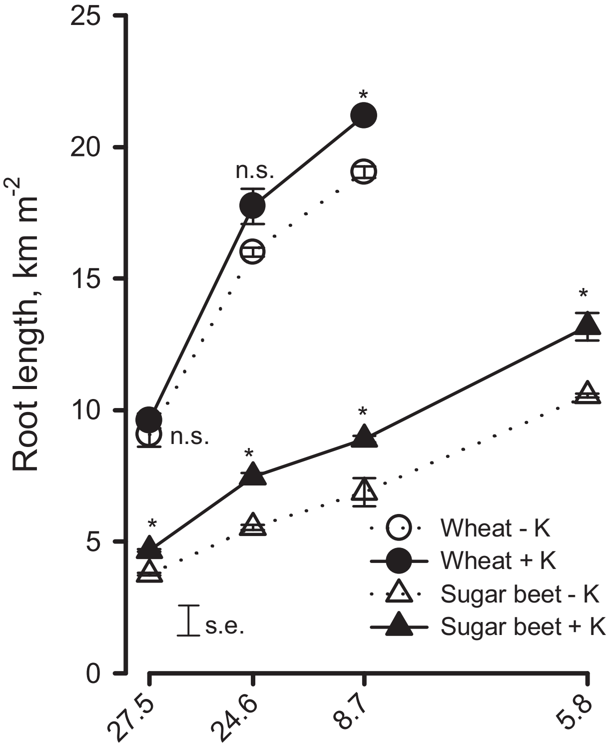


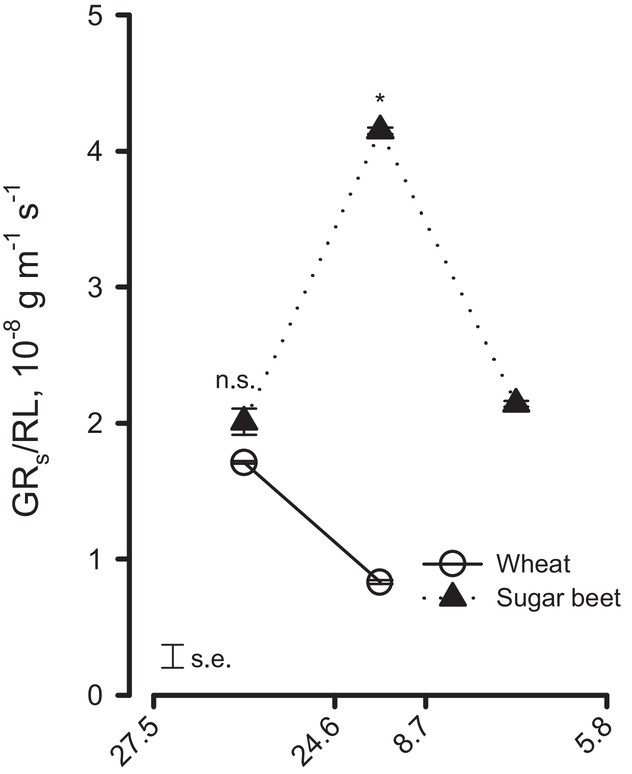
Fig. 4: *Root length of spring wheat and sugar beet in a soil depth 0-90 cm grown on a sandy clay loam in the field with (+K) and without (-K) K fertilisation. n.s. no significant difference (p< 0.05) between (+K) and (-K) treatments. * significant differences (p< 0.05) between (+K) and (-K) treatments.*

Root length (RL)

Root length of wheat and sugar beet with (+K) and without (-K) fertilisation over the whole growth period is shown in figure 4. Wheat reached a total root length of 21 and 19 km m^{-2}, in July, on the fertilised and unfertilised treatments, respectively. At all harvests sugar beet produced only 34 to 48 % of the total wheat root system, with a maximum of 13 and 10 km m^{-2}, in August, on the fertilised and unfertilised treatments, respectively.

Shoot growth rate root length ratio (GR_s/RL)

The shoot growth rate to root length ratio (GR_s/RL) is a measure of the demand for nutrients the growing shoot is putting on the roots. The greater this ratio the higher is the demand on the roots. Figure 5 shows the GR_s/RL ratio of wheat and sugar beet on fertilised treatments, where K was not limiting growth and the plants were growing optimally. This means the K uptake was not restricted and the plants could take up enough K to meet their requirement, which represents the K demand to be met by the roots. A direct comparison between the crops for nutrient demand is difficult, since at the various growing periods the plants were at different growth stages.



<u>Fig. 5</u>: *Shoot growth rate (GR_s) in relation to root length (RL) of spring wheat and sugar beet grown on a sandy clay loam at optimum K fertilisation. n.s. no significant difference ($p< 0.05$) between plant species.* significant differences ($p< 0.05$) between plant species.*

However, the highest value for sugar beet was more than twice that of wheat, which is to be expected because of its faster growing shoots (Fig. 3) and smaller root system (Fig. 4). This means sugar beet puts a higher demand for K uptake on the roots than wheat.

Total K uptake and influx

Total K uptake in the dry matter is a measure for the ability of plants to acquire K from the soil and accumulate it in the shoots. It is the product of dry matter yield and K concentration in dry matter. Differences of K concentration in plants and of dry matter production resulted in 2 times higher total K uptake of sugar beet in comparison to wheat on both fertilised and unfertilised plots (Fig. 6). The K uptake followed a similar pattern for both crops, being low at the early growth stages increasing with time and reaching a maximum of 151 and 227 kg ha^{-1}, in July, with and without fertilisation, respectively, for wheat, thereafter no net uptake took place. Sugar beet with a maximum of 259 and 412 kg ha^{-1} on unfertilised and fertilised treatments, in August, had a 70-80 % higher total K uptake than wheat.

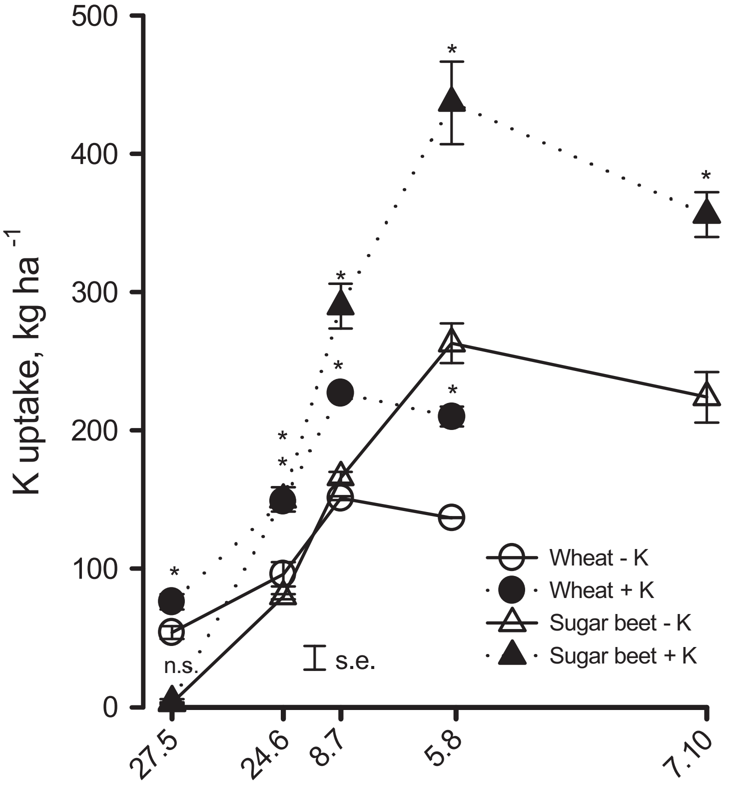


Fig. 6: *Total K uptake of spring wheat and sugar beet grown on a sandy clay loam in the field with (+K) and without (-K) K fertilisation. n.s. no significant difference (p< 0.05) between (+K) and (-K) treatments.* * *significant differences (p< 0.05) between (+K) and (-K) treatments.*

At limiting soil K supply the influx is a measure for the physiological capability of the roots to extract K from soil. The influx increased with plant age from 25 x 10^{-14} and 34 x 10^{-14} mol cm^{-1} s^{-1}, in the growth period 27.5-24.6, to a maximum of 53 x 10^{-14} and 56 x 10^{-14} mol cm^{-1} s^{-1}, in 24.6-8.7, for sugar beet fertilised and unfertilised treatments, respectively, then decreased for both treatments (Fig. 7). These values corresponded to 2 times higher influx in comparison to wheat on both treatments, in 27.5-24.6, and 10 and 8 times higher influx on the unfertilised and fertilised treatments, respectively, in 24.6-8.7, (Fig. 7). The highest influx for wheat was 13 x 10^{-14} and 17 x 10^{-14} mol cm^{-1} s^{-1} with and without fertilisation, respectively.

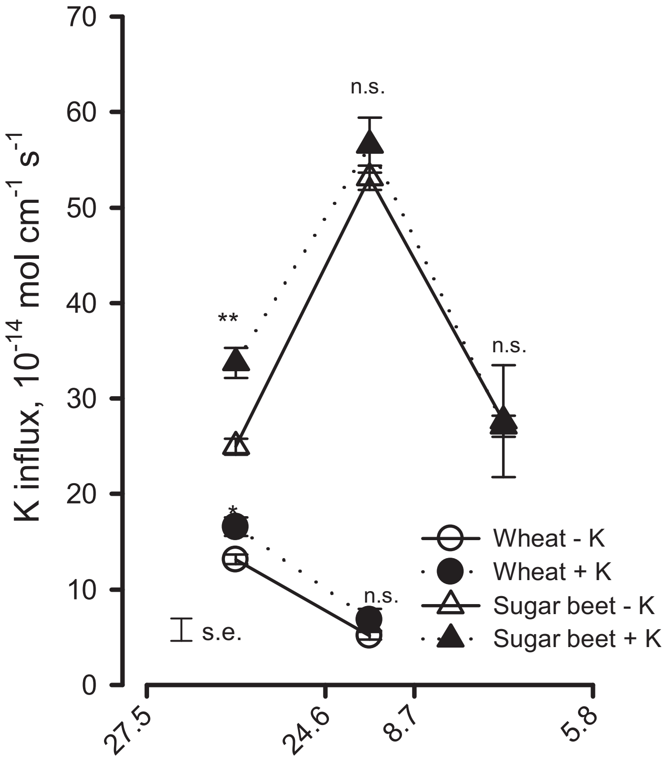


Fig. 7: *Potassium influx of spring wheat and sugar beet grown on a sandy clay loam in the field with (+K) and without (-K) fertilisation. n.s. no significant difference ($p < 0.05$) between (+K) and (-K) treatments.* significant differences ($p < 0.05$) between (+K) and (-K) treatments.*

Discussion

In the last chapter, it was shown that sugar beet had a very high uptake efficiency, which was because of an exceptionally high net influx even under sub-optimal soil solution K concentrations. However, the experiment was conducted under controlled conditions, whereas for plants growing under field conditions characterisation of nutrient supply has to encounter several uncertainties, related to nutrient loss and dependence of their availability on soil and climatic conditions as well as water supply (Sauerbeck and Helal, 1990). Plants growing in the field are growing naturally, and are subjected to environmental, physical and biological factors and their interactions. Hence, investigating nutrient efficiency in the field allows for more practical results obtained under natural conditions. Since, for example, all physical and chemical soil factors influence root morphological development and physiological activity, consequently, has a direct effect on nutrients uptake efficiency. Accordingly the plants might exhibit varying nutrient efficiency under natural as compared to controlled growing conditions. The objective of this study was to investigate the K efficiency of wheat and sugar beet under natural conditions, and to identify the varying mechanisms or factors behind their efficiency.

Considering the relative yield, sugar beet was as K efficient as wheat, producing up to 76 % of the beet yield without fertilisation relative to fertilised yield. These findings contrast with those of Claassen (1994) who concluded in a field experiment that sugar beet was less K efficient than wheat, since it obtained only 80 % relative yield, whereas wheat had 100 % relative yield. The results are in partial agreement with those of Kuhlmann (1983) who, regardless of the K content in soil or plant, did not detect any significant increase in grain yield of wheat due to varying fertilisation levels, but beet yield was increased significantly.

The fact that sugar beet leaves dry matter yield on unfertilised treatments, tended to be higher than that on fertilised ones (Fig. 1), could be explained by the role played by K in the rate of mass flow-driven solute transport in the sieve tubes. The transport rates of the photosynthates from source to sink are much lower in K-deficient, as compared to K-sufficient plants (Marschner, 1995). Hence, the slower transport of the photosynthesis products led to their accumulation in the leaves, and thus the observed increase in leaves yield in the K deficient plants. Also considering the grain yield of wheat, which was not significantly lower on unfertilised as compared to fertilised treatments (Fig. 1), but the former treatments had significantly higher K concentration in grains as compared to the latter treatment (Fig. 2). Here we found that the affected yield component was the thousand grain weight, which was significantly lower in (-K) plants as compared to (+K) plants (data not shown). This is also because of the disturbed transport rates of solutes in the phloem due to K deficiency.

Efficient plant species employ specific physiological mechanisms to increase the effectiveness of nutrient utilisation (Sattelmacher et al., 1994), for example, they possess lower internal nutrient requirements or require less concentration of the nutrient in question in the plant tissues for dry matter production. In this experiment, the internal K requirement to produce 80% of maximum yield, was between 3.5-5.0 % for sugar beet and 2.0-3.0 % for wheat (Fig. 2). These values are lower than those of Kuhlmann (1983) who reported about 4.2 % K in wheat dry matter at the stage of shoot elongation, and between 4.5-6.0 % in sugar beet dry matter at full expanded leaf stage. The results agree with the values given by Bergmann (1993) for K concentration in dry matter required for optimum dry matter yield, which are 3.5-6.0 % for sugar beet and 2.9-3.9 % for wheat at comparable growth stages. However, the data show that in this experiment, the K concentrations in dry matter, although within the range of the needed K concentration, but were on the lower part of the range, indicating that the availability of K was low. These results and those cited from the literature show that wheat is more efficient in utilising K for dry matter production as compared to sugar beet.

Nutrient amount and mobility in the soil as well as acquisition characters of the plant such as the root size, uptake kinetics and mobilising ability of the root system control nutrient supply to the plants (Jungk and Claassen, 1997). A large root system as well as alteration of root geometry could be considered as one of the strategies developed by plants for a high uptake efficiency (Rengel, 1999). This could be the mechanism for wheat efficiency, especially so, that for both treatments around 80% of the root system was produced before flowering, in June, (Fig. 4). During this time the most active vegetative growth took place and the highest amount of K was needed. Claassen (1994) showed that not only the root size is important for wheat K efficiency, but also that the highest shoot growth in June and July occurred with a completely developed root system capable of acquiring the necessary K needed for growth by exploiting a larger soil volume for K. As could be seen from the above data, the efficiency of sugar beet could not be attributed to a large root system, since it had only 34-48 % of the root length of wheat, over the whole growth period.

Plant growing tissues are sinks for photosynthetic products and mineral nutrients (Clarkson and Hanson, 1980). Sauerbeck and Helal (1990) suggested that root development and physiological activity is controlled by the shoots, since nutrient uptake by the roots, translocation to the shoots and subsequent redistribution in the different plant organs is controlled by complex communications between shoots and roots. Caradus and Snaydon (1986) reported that shoot systems can have large effects on nutrient uptake, if only by the demand for nutrients that they impose. Faster growing shoots require more nutrients as compared to slower growing ones. Sugar beet had a much higher shoot growth rate as compared to wheat (Fig. 3). Steingrobe and Claassen (2000) reported that during a time interval, the nutrient content of already grown plant parts is nearly constant and thus causes no demand for nutrient uptake. At optimum nutritional status, the demand for nutrients imposed on the roots is caused mainly by the new shoot growth. As such changes in root growth pattern, in response to nutrient deficiency, are better described by the ratio of shoot growth rate to root length than by root length-shoot weight or shoot weight-root length ratios. As was shown in the GR_s/RL ratio, sugar beet had much higher demand for nutrient acquisition, which means the roots had to exert more effort for K acquisition to meet the shoot demand (Fig. 5). The lower shoot growth rate and large root system of wheat mean a lower nutrient uptake demand to be met by a unit of root. Nevertheless, sugar beet proved to be as K efficient as wheat.

Considering the absolute dry matter yield, sugar beet produced much higher dry matter (150 and 70 dt ha^{-1}) beet and leaves, respectively, as compared to wheat (45 and 77 dt ha^{-1}) grain and straw, respectively, (Fig. 1). As was shown in the results, sugar beet had higher K concentrations in dry matter (Fig. 2) because of its higher internal requirement. Consequently, sugar beet had double the total K uptake of wheat (Fig. 6), since total K uptake is the product of dry matter and K concentration in dry matter. Hence, it is obvious that sugar beet had a higher uptake efficiency than wheat. As is seen, this high uptake efficiency of sugar beet can not be attributed to a large root system (Fig. 3), instead can only be explained by the high uptake efficiency of the single roots or acquisition rate per unit of root and time, i.e. the influx. The results of this study showed that to meet the demand for nutrient acquisition imposed by the fast growing shoots, sugar beet increased its uptake rates per unit root and time considerably. It had 2 and 10 times higher influx as compared to wheat, on the unfertilised treatments, in the growth periods 27.05-24.06 and 24.06-08.07, respectively. Especially at the growth period 24.06-08.07, with the highest demand for K acquisition on the roots (Fig. 5), sugar beet had nearly 2 times higher influx as compared to the growth periods 27.05-24.06 and 08.07-05.08, respectively, (Fig. 7). Claassen (1994) showed that by similar soil solution K concentration, sugar beet influx was 3 times higher in July than in June, and that the higher shoot growth rate in July, representing a higher K demand on the roots, was covered by a higher influx. Caradus and Snaydon (1986) suggested that plants with small root systems had high uptake rates per unit length because uptake per plant is determined by shoot factors.

The influx realised by sugar beet was relatively high for the very low measured soil solution concentrations (Appendix Table 2), and transport to the roots would probably limit K uptake (Jungk and Claassen, 1997; Claassen and Steingrobe, 1999). Hence, it remains to be answered what enabled sugar beet to achieve a higher influx as compared to wheat, even though the transport of K to the roots was limiting K uptake. A possible explanation to the higher influx of sugar beet could be that it might have caused chemical changes in the rhizosphere through root exudates, which released non-exchangeable K into the soil solution. Several workers reported the significance of chemical mobilisation of mineral nutrients in the rhizosphere by plant roots, for example, of phosphate and micro-nutrients for plant nutrition (Marschner et al.,1986; Gerke et al., 1994; Rengel et al., 1998). Little information exists about K mobilisation by root exudates, for example, by organic acids (Meyer, 1993).

More can be said to these aspects after model calculations which will be performed and discussed in the next chapter.

Conclusions

1- Sugar beet was similarly K efficient as wheat, that is both produced about 80% on the unfertilised as compared to fertilised plots.

2- Wheat efficiency could be attributed to a large root system and a high utilisation efficiency or low internal K requirement.

3- Sugar beet, even though it had a small root system, a higher shoot growth rate and a high internal requirement had a similar K efficiency as wheat because of a high efficiency of the single root or influx.

4- It remains to be investigated why under limiting K supply, sugar beet was able to achieve a higher K influx than wheat.

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Table 1 *Exchangeable K in different soil depths (0-90 cm) under sugar beet and wheat grown on a sandy clay loam in the field over the whole growth period in 1997*

Plant species	Month	Soil depth (cm)							
		0-15	15-30	30-60	60-90	0-15	15-30	30-60	60-90
		Exchangeable K concentration µmol kg^{-1} soil							
		-K (since 1976)				+K (1976-1986)			
Sugar beet	27 May	1351 a* (26)	1056 b (27)	999 b (47)		1609 a (52)	1477 a (142)	1053 a (140)	
	24 June	941 a* (37)	674 b* (9)	350 c* (28)		1396 a (36)	1216 a (62)	388 a (9)	
	8 July	574 a* (9)	505 a* (29)	166 b (29)		1027 a (73)	773 a (29)	191 b (0.1)	
	5 Aug.	962 a* (26)	940 ab (173)	560 b (10)	440 b (37)	1258 a (35)	1253 a (55)	562 b (17)	498 b (11)
	7 Oct.	575 a* (25)	573 a* (17)	234 b* (16)		1243 a (218)	760 ab (8)	381 b* (21)	
Wheat	27 May	1177 a* (8)	1031 b* (8)	730 c (18)		1601 a (170)	1160 b (25)	851 b (46)	
	24 June	600 a* (27)	579 a (9)	484 a* (18)		832 a (18)	398 b (44)	264 b (27)	
	8 July	609 a (0.1)	402 b* (18)	175 c* (39)	147 d* (18)	745 a (93)	306 b (9)	208 bc (38)	177 c (35)
	5 Aug.	737 a* (53)	554 ab* (64)	427 b (29)		1204 a (81)	844 b (25)	461 c (29)	

Within treatments, specific dates and soil depths, values followed by different letters are significantly different after Tukey ($p < 0.05$).

*Significant differences ($p < 0.05$) between treatments and within similar soil depths after Tukey.

Values between brackets represent the standard error of means.

Table 2: *Soil solution K concentration in different soil depths (0-90 cm) under sugar beet and wheat grown on a sandy clay loam in the field over the whole growth period in 1997*

Plant species	Month	Soil depth (cm)							
		0-15	15-30	30-60	60-90	0-15	15-30	30-60	60-90
		Soil solution K concentration µmol L^{-1}							
		-K (since 1976)				+K (1976-1986)			
Sugar beet	27 May	10.4 a* (1.2)	9.99 a* (1.5)	5.12 a (0.8)		23.3 a (0.6)	18.0 b (0.7)	7.03 c (0.9)	
	24 June	4.54 a* (0.2)	1.43 b* (0.2)	1.79 b (0.5)		14.3 a (0.8)	6.30 b (0.5)	1.98 c (0.2)	
	8 July	4.06 a* (0.3)	3.02 a* (0.3)	2.54 a (0.2)		7.67 a (0.2)	5.13 b (0.4)	2.71 c (0.1)	
	5 Aug.	3.56 a* (0.3)	2.90 ab* (0.6)	2.31 ab* (0.3)	1.44 b (0.3)	6.73 a (0.3)	5.80 a (0.3)	4.64 ab (1.1)	1.97 b (0.4)
	7 Oct.	2.50 a* (0.3)	2.48 a* (0.3)	1.83 a* (0.01)		7.86 a (0.7)	4.54 b (0.3)	3.13 c (0.01)	
Wheat	27 May	6.45 a (0.6)	3.63 b (0.1)	1.12 b* (0.1)		7.05 a (0.2)	3.98 b (0.4)	3.27 c (0.3)	
	24 June	2.84 a (0.2)	2.19 a (0.2)	2.56 a (0.1)		4.12 a (0.4)	2.58 a (0.1)	2.39 a (0.4)	
	8 July	4.11 a (0.1)	3.44 a (0.7)	2.81 ab (0.5)	1.90 b (0.7)	4.92 a (0.1)	3.62 a (0.2)	2.70 ab (0.2)	2.09 b (0.5)
	5 Aug.	4.80 a (0.2)	2.43 b* (0.1)	2.79 b* (0.1)		6.25 a (0.6)	4.21 a (0.1)	3.85 a (0.5)	

Within treatments, specific dates and soil depths, values followed by different letters are significantly different after Tukey ($p < 0.05$).

*Significant differences ($p < 0.05$) between treatments and within similar soil depths after Tukey.

Values between brackets represent the standard error of means.

Chapter 5

Calculated K Uptake and Simulation of K Dynamics of Different Plant Species Under Controlled and Field Conditions

Abstract

In the previous two chapters, sugar beet because of a high influx, proved to be as K efficient as wheat, which had a large root system and low internal K requirement. At K deficiency conditions, these mechanisms were not sufficient to explain the actually measured K uptake especially so by sugar beet. Hence, the K transport in soil and uptake by the plants, under the previous experiments conditions, were simulated by a mechanistic model which encompasses uptake by root hairs as well. The objective was to compare simulated and actual K uptake of the different plant species, under different growth conditions and K concentrations in the soil solution, in an attempt to understand the underlying mechanisms of nutrient uptake by these plant species.

To quantify the significance of single soil and plant parameters for nutrient uptake a sensitivity analysis was carried out. Soil and plant parameters used for K uptake simulation were obtained from different plant species grown on a "K fixing" sandy clay loam, at various soil solution K concentrations, obtained by fertilisation, both under controlled and field conditions.

Under sufficient K in the soil solution (C_{Li}), where transport was not limiting uptake, the model predicted the actual K uptake correctly. At deficient K concentrations, the model over-predicted the K uptake by both cereals but under-predicted that of sugar beet. The calculated concentration profiles around the roots showed that for cereals, wrong values of the uptake kinetics caused the over-prediction of K uptake, whereas for sugar beet some process more than was considered by the model took place. In the field experiment the simulation model was able to calculate only 34 % of the measured sugar beet uptake throughout the growing period. The lowest calculated K influx (only 9 % of measured value) corresponded, to the period of June 24th -July 8th, of highest actual uptake.

Sensitivity analysis showed that, under low K concentrations, the soil solution K concentration (C_{Li}) was the most important factor controlling K uptake, especially for sugar beet. This indicates that roots may have increased the K concentration in soil solution by chemical mobilisation. Research is needed to understand the mechanism by which this is achieved.

Introduction

It was shown in chapter 3 and 4, that sugar beet and wheat are K efficient species. The K efficiency was investigated under controlled and field conditions. Sugar beet efficiency was attributed to a very high net influx, whereas that of wheat was due to a large root system and low internal K requirement. However, it was not clear whether these mechanisms were enough to explain the actually measured uptake, especially by sugar beet. To clear these points the K transport in soil and uptake by plants, under the experiments conditions, were simulated by a mechanistic model. To explain the significance of single soil and plant parameters for K uptake, a sensitivity analysis was conducted, and the results are shown and discussed in this chapter.

Nutrient uptake of plants from the soil results from interactions occurring at the soil-root interface (Claassen et al., 1986). It is a complex sequence of steps including desorption of ions from the solid phase, movement of nutrients towards an absorbing root, transport of ions through the membranes of the root cells towards the root xylem vessels and transport to the shoot (Claassen and Steingrobe, 1999). As such it is influenced by various soil and plant parameters and their interactions.

Nutrient simulation models are helpful to improve the understanding of the processes governing soil supply and plant uptake of mineral nutrients. These models fall into two general categories. Empirical models (Yerokun and Christenson, 1990), which describe observed phenomena by statistical means and regressions without trying to explain how they happen. They describe input-output relations not taking into account the underlying processes and as such are often called black-box models (Claassen and Steingrobe, 1999). The other category includes the mechanistic models (Nye and Marriot, 1969; Claassen and Barber, 1976; Cushman, 1979; Claassen et al., 1986; Claassen, 1990b), which try to explain how observed phenomena have happened by means of basic biophysical, biochemical and physiological mechanisms, and mathematical description of the underlying processes (Rengel, 1993; Claassen and Steingrobe, 1999). Mechanistic models provide valuable means for calculating the nutrient uptake from soils as affected by the involved soil and plant factors, and assessing the significance of individual soil and plant parameters (Claassen et al., 1986). They enable testing the correctness of our concepts about the interactions between plant and soil with regard to nutrient uptake, by comparing modelled and observed results. This shows areas where more research is needed, and gaining access to calculating not easily measurable data (Claassen and Steingrobe, 1999).

In this study the model of Claassen (1994) which encompasses nutrient uptake by root hairs as well, is used to simulate K uptake of different plant species. The model is based on three steps: a) desorption of nutrients from the soil solid phase, b) transport of nutrients to roots by mass flow and diffusion (Barber, 1962), c) nutrient influx into the root as a function of the nutrient concentration in the soil solution at the root surface. This can be described by a modified Michaelis-Menten equation derived from enzyme kinetics, and applied by Epstein and Hagen (1952) and modified by Nielsen (1972).

The aim of this study was to compare simulated and actual K uptake of different plant species, under different growth conditions and K concentrations in the soil solution, in order to try to explain the underlying mechanisms of nutrient uptake by these plant species. To simulate nutrient uptake, soil and plant parameters were obtained from different plant species grown on a sandy clay loam, at various soil solution K concentrations. Wheat (*Triticum aestivum* L. cv. Star), barley (*Hordeum vulgare* L. cv. Madras) and sugar beet (*Beta vulgaris* L. cv. C+T) were grown in the growth chamber, under controlled conditions. Wheat cv. Star and sugar beet cv. Kawetina were grown under field conditions in Bavaria, southern Germany.

Materials and Methods

Soil and plant parameters for calculating K uptake were obtained from a pot experiment under controlled conditions and a field experiment. Both experiments were conducted with Anglberg sandy clay loam soil, having pH 7.2, 33 % clay, 31 % silt and 3.8 % organic carbon.

Pot experiment

Spring wheat cv. Star, spring barely cv. Madras and sugar beet cv. C+T were grown in a growth chamber with a day/night regime 16/8 hours, temperature 25/18 °C and relative humidity 70%. The photosynthetic active radiation during the day time was 250 µE m^{-2} s^{-1}. Four K levels 0, 0.6, 2.4 and 4.8 g kg^{-1} soil were added as KCl. These fertilisation levels corresponded to a soil solution K concentration of 5 µM (K1), 29 µM (K2), 2.65 mM (K3) and 10 mM (K4), respectively. The plants were watered daily to a soil water content of 34% by weight. Three pots per treatment were left unplanted as control for measurement of soil parameters. The treatments were replicated 3 times. Total number of plants grown for the first, second, and third harvest, respectively, were 10, 5 and 5 for wheat and barely and 10, 3 and 3 for sugar beet. First harvest was 16, second harvest 24 and third harvest 31 days after sowing. After each harvest shoot dry weight was determined after drying the plants at 105 °C to constant weight. Potassium content of shoot dry matter was measured by flame photometry after wet digestion in a mixture of concentrated tri acid (HNO_3, $HClO_4$, and H_2SO_4 in a volumetric ratio of 8:2:1, respectively). The roots in the whole pot were separated from the soil by washing them gently over a 0.2 mm sieve and root length was determined using a line intersection method Tennant (1975). The mean root radius (r_0) was calculated using the following equation, assuming that the specific weight is 1 g cm^{-3}:

$$r_0 = \sqrt{\frac{RFW}{\Pi RL}} \qquad (cm) \qquad [1]$$

where:

RFW= root fresh weight (g or cm^3)

RL = root length (cm)

Assuming that the roots are regularly distributed in the soil, the average half distance between neighbouring roots (r_1) was calculated using the root length density (RL_v), (RL_v = RL per soil volume of the pot):

$$r_1 = \sqrt{\frac{1}{\Pi RLv}} \qquad (cm) \qquad [2]$$

Soil solution was obtained by the displacement method of Adams (1974) and K concentrations were determined by flame photometry. For measuring exchangeable K one g moist soil was extracted 5 times with 10 mL 1 M NH_4OAc solution (pH 7) at 15 minutes intervals. The K concentration in the extract was determined by flame photometry. The soil exchangeable K content was calculated on dry weight basis. The K influx was calculated after Williams (1948). For more details see chapter 2.

Field experiment

In the field data were obtained from a long term fertiliser experiment on a "K fixing" soil in Bavaria, southern Germany, in which K fertilisation rates varied from 0 to 1000 kg K ha^{-1} $year^{-1}$. These treatments were applied from 1976 through 1986. In 1997, spring wheat cv. Star and sugar beet cv. Kawetina were sown on 50 m^2 plots, on the 13th of March and 04th of April, respectively. Before sowing 43 kg P ha^{-1} and 80 kg N ha^{-1} were applied to the soil as super-phosphate and ammonium sulphate and ammonium nitrate. Harvests were carried out on 27th May, 24th June, 08 th July , 05 th August for both crops and on 07 th October for sugar beet. At each harvest date, 3 sub-samples of plants, roots and soil of each species were taken from random areas of the plots from the 0 kg K fertilised (-K) and highest fertiliser level of 1000 kg K ha^{-1} (+K) treatments. The same plant and soil parameters as for the pot experiment were determined. For more details see chapter 4.

Model description

Transport of nutrients to the root is by mass flow (F_M) and diffusion (F_D) (Barber, 1962). Mass flow is the convective movement of nutrients dissolved in soil solution towards the roots as a result of shoot transpiration. Diffusion occurs along a concentration gradient and results from spontaneous oscillation of ions and molecules driven by thermal agitation (Claassen and Steingrobe, 1999). Figure 1 shows the major processes involved in nutrient transport and uptake. In the first step, plants take up nutrients according to Michaelis-Menten kinetics (Fig. 2) and water due to transpiration. If nutrients transported by mass flow are less than taken up by the root, the concentration at the root surface decreases. Then as a second step, transport to the roots along the concentration gradient results.

The nutrient transport can be calculated as follows:

a) mass flow (F_M) given by the product of water flux (v) and the concentration of the nutrients in soil solution (C_L)

$$F_M = vC_L$$

b) Diffusion (F_D) governed by the diffusion principles of Ficks first law

$$F_D = -D_e \cdot \frac{dC}{dx}$$

D_e = effective diffusion coefficient, $cm^2\ s^{-1}$

$\frac{dC}{dx}$ = concentration gradient (often simplified as $\frac{\Delta C}{\Delta x}$)

Total nutrient flux (F_T) to the roots is the sum of mass flow and diffusion

$$F_T = F_M + F_D$$

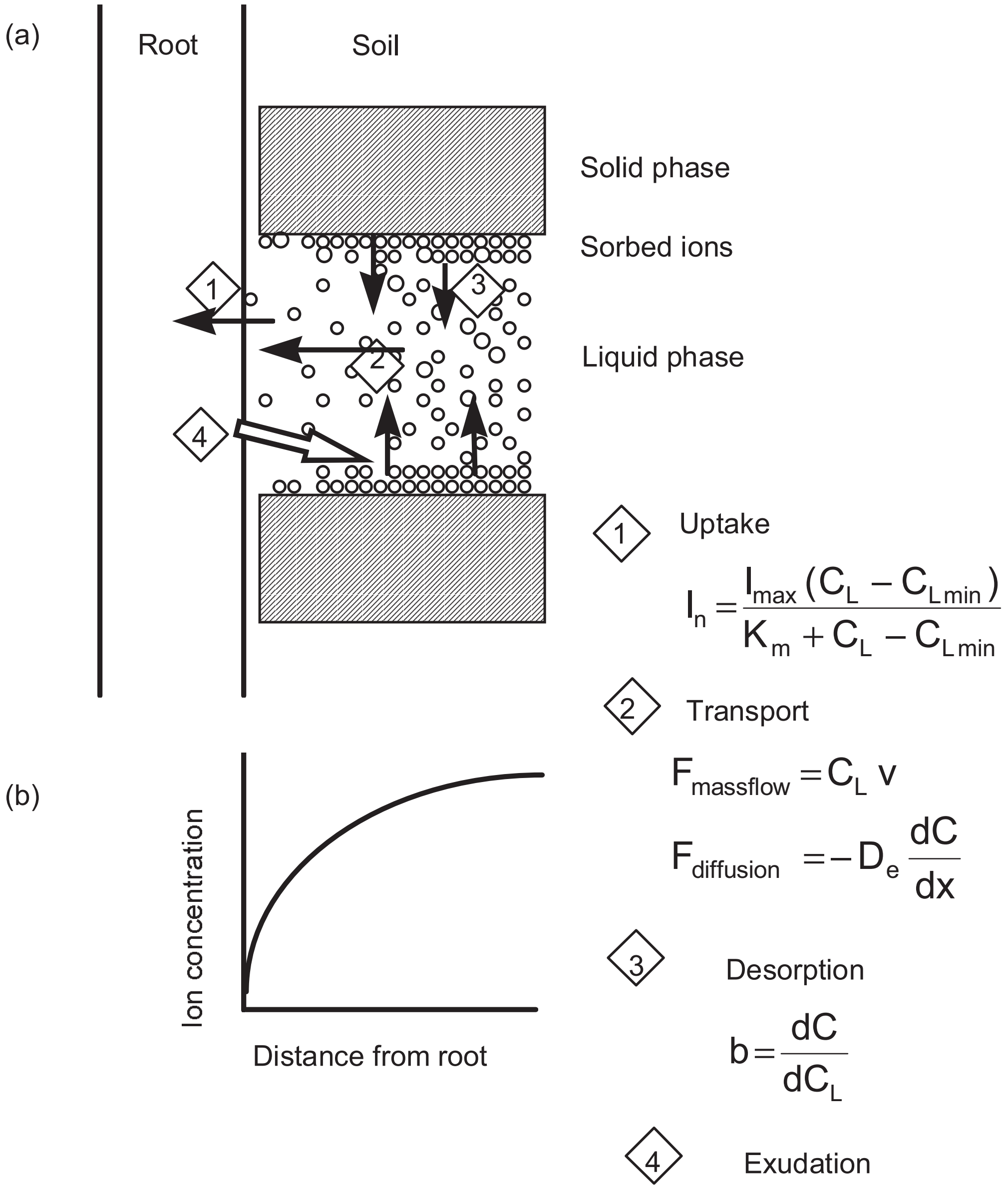

Figure 1 ***(a)*** *The Soil-Root System Consisting of the Root Surrounded by the Soil Solid Phase with Sorbed Ions and the Pore Space Filled with Liquid. Circles symbolise ions. Shown are the main processes of nutrient transport and uptake. (b) Concentration profile of an ion in the rhizosphere as shown in (a) (from Claassen and Steingrobe (1999), modified).*

Decreasing the concentration of the soil solution through K uptake by plants disturbs the equilibrium between K ions sorbed to the solid phase and dissolved ions in soil solution. This leads to the third step, namely, desorption according to the buffer power (b) of the soil, which describes the relation between changes in the total amount of available or diffusible K (dC) and changes in solution concentration (dC_L) (Jungk and Claassen, 1997; Claassen and Steingrobe, 1999; Steingrobe and Claassen, 2000). Diffusion occurs essentially in the soil liquid phase, hence, the volumetric water content (Θ) and the tortuosity of the water filled pores influence diffusion by affecting the effective diffusion coefficient (D_e), used for calculating the diffusive flux (F_D) according to the equation:

$$D_e = D_L \Theta f \frac{1}{b}$$

D_L= diffusion coefficient in water

f = impedance factor

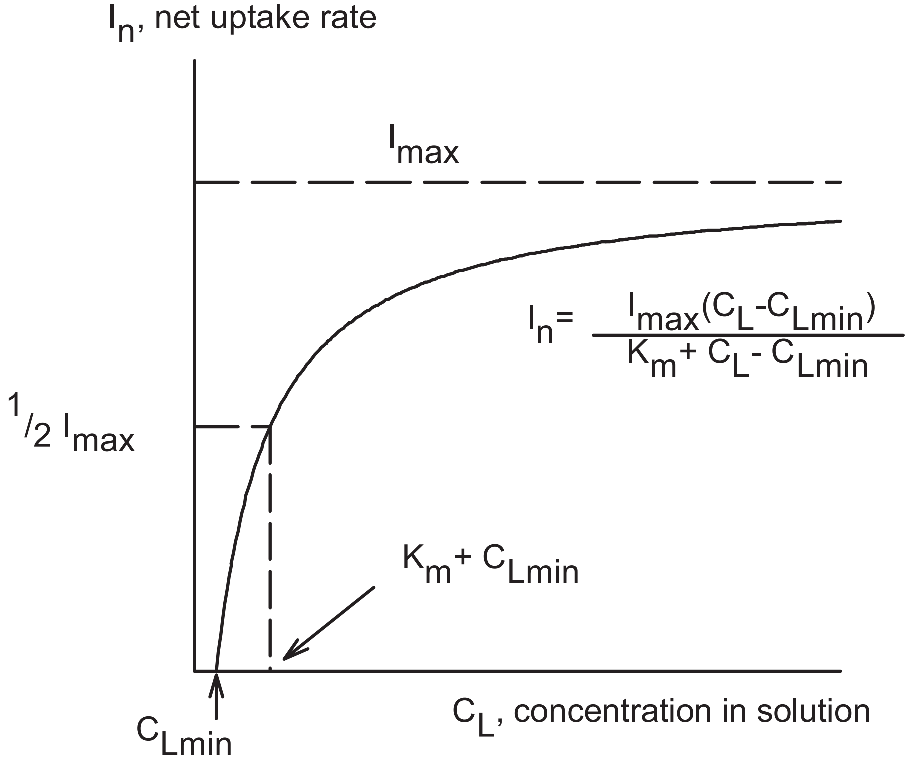

Figure 2 *Relation between Soil Solution Concentration at root surface (C_L) and net uptake rate (In) described by the Michaelis-Menten Kinetics (from Claaassen and Steingrobe (1999)).*

Because of mass conservation nutrient flux to the root surface (F_T) must be equal to the net influx (In) into the roots. Hence, K uptake is a function of plant and soil characteristics and their interactions. Integrating the given equations develops a mathematical model which enables calculating K uptake and K dynamics in the rhizosphere (Claassen, 1990b; Jungk and Claassen, 1997; Claassen and Steingrobe, 1999).

The fourth step in nutrient transport and uptake processes (Fig. 1) is root exudation, which is not included in the model used in this research. Plants change the chemistry of the rhizosphere by changing the pH through exudation of H^+, by root exudates, which comprise both high and low molecular weight compounds and by interactions with micro-organisms and/or their exudates (Marschner et al., 1986). Chemical mobilisation of nutrients in the rhizosphere by plant roots can substantially change the availability of, for example, phosphate and micro-nutrients (Cakmak et al., 1994; Beißner and Römer, 1998; Rengel et al., 1998).

Determination of plant and soil parameters used for nutrient uptake simulation

Transport parameters

C_{Li}	The initial K concentration in the soil solution. C_{Li} was obtained by the displacement procedure, after Adams (1974), in the un-planted soil (pot experiment) or from planted soil at the start of the modelling period (field experiment).	mol cm^{-3}
b	buffer power defined as the ratio of the changes in diffusible K, that is increase in exchangeable K, due to fertilisation, to soil solution concentration (dC/dC_L). For example, the addition of 20 µmol K per cm^3 soil increased exchangeable K by 0.6 µmol per cm^3 soil and C_{Li} by 0.014 µmol per cm^3. This resulted in a buffer power (b) of 43.	
D_L	The diffusion coefficient of K in water at 25 °C (1.98 x 10^{-5}) Pearson (1966).	$cm^2\ s^{-1}$
Θ	volumetric water content of the soil.	$cm^3\ cm^{-3}$
f	impedance factor ($f=0.97\ \Theta-0.17$) Kaselowsky (1990).	
V_0	water influx calculated by dividing the transpiration rate by the root root surface area. In the pot experiment the transpiration was measured, in the field transpiration was assumed as 5L m^{-2} day^{-1}.	$cm^3\ cm^{-2}\ s^{-1}$

Root parameters

Uptake-kinetics

I_{max}	maximum influx theoretically achieved at infinite concentration. The I_{max} were calculated from the highest influx measured at the highest K level multiplied by different factors. These factors were obtained from Meyer (1993), who found that the I_{max} of K deficient plants was higher than that of those at sufficient K by factor 2 to 6 depending on the C_{Li}. For example, wheat K influx at the high K fertilisation, in the pot experiment, was 10.5 x 10^{-14} mol cm^{-1} s^{-1}. At a C_{Li} 5 µM, I_{max} was calculated by multiplying this highest influx by factor 5. This factor was found by Meyer (1993) at a comparable C_{Li}. Another example shows that the highest influx between the 1st and 2nd harvests, for wheat, was 3.75x10^{-14} mol cm^{-1} s^{-1}. This was multiplied by factor 1.2, a factor reported by the author for wheat at a comparable C_{Li} of around 2.3 µmol per cm^3 solution. In the field, the highest influx of wheat was 8.43 x 10^{-14} mol cm^{-1} s^{-1}. This was multiplied by factor 8 also after Meyer (1993) at a comparable C_{Li} of around 2.4 µmol x 10^{-9}	mol cm^{-2} s^{-1}
K_m	Michaelis constant is the concentration that allows uptake at half I_{max} minus C_{Lmin}, values were taken from Meyer (1993).	mol cm^{-3}
C_{Lmin}	minimum solution concentration at which influx equals efflux, or net influx equals zero. Values were taken from Meyer (1993).	mol cm^{-3}

Geometry

r_0	root radius determined as described earlier.	cm
r_1	average half distance between neighbouring roots, see	cm
RL_1	root length at first harvest.	cm
k	growth rate constant of roots.	
	Exponential growth in pot experiment	d^{-1}
	Linear growth in the field.	cm m^{-2} d^{-1}

Root Hairs

N	number of root hairs per cm root taken from Claassen (1994).	
r_1h	average half distance between neighbouring root hairs, from Claassen (1994).	cm

Parameters used for calculating uptake under controlled and field conditions are presented in the appendix.

Model output

The model calculates the nutrients depletion around a single root as a function of time of uptake. It also calculates the uptake and influx at given time steps of a unit root length and of a growing root system.

Potassium uptake in the field was calculated for each soil depth (0-15, 15-30, 30-60, 60-90) cm separately and the total K uptake was obtained by summing up the uptake from single layers. The calculated influx was obtained by dividing the total uptake by the average root length and time.

Results

Pot experiment

The measured K influx of the different plant species at 2.65 mM, was nearly 10 times higher than that measured at the deficient soil solution concentration of 5 µM. Furthermore, at limiting K supply (5 µM), sugar beet had always a higher influx than both wheat and barley (Fig. 3a and Fig. 4a).

At the highest C_{Li} of 2.65 mM, calculated and measured influx for all three species were similar, that is actually measured influx was closely predicted by the model (Fig. 3a). The fact that the model predicted the measured influx by all tested plant species correctly, indicates that transport by mass flow and diffusion was not limiting uptake and the K influx was determined by I_{max}. This means, at sufficient K in the C_{Li}, the model defined the mass flow, diffusion and the Michaelis-Menten kinetics.

As indicated by the flat concentration curves (Fig. 3b), K was taken up from the whole soil volume around the roots and the concentrations at the root surface and between the roots remained very high throughout the growth period. The ΔC_L was 100 to 440 µM for the different plant species. The C_{Li} of wheat and barley was lower than that of sugar beet and because of a higher I_{max}, the latter was able to lower C_{L0} further than the cereals (Fig. 3b).

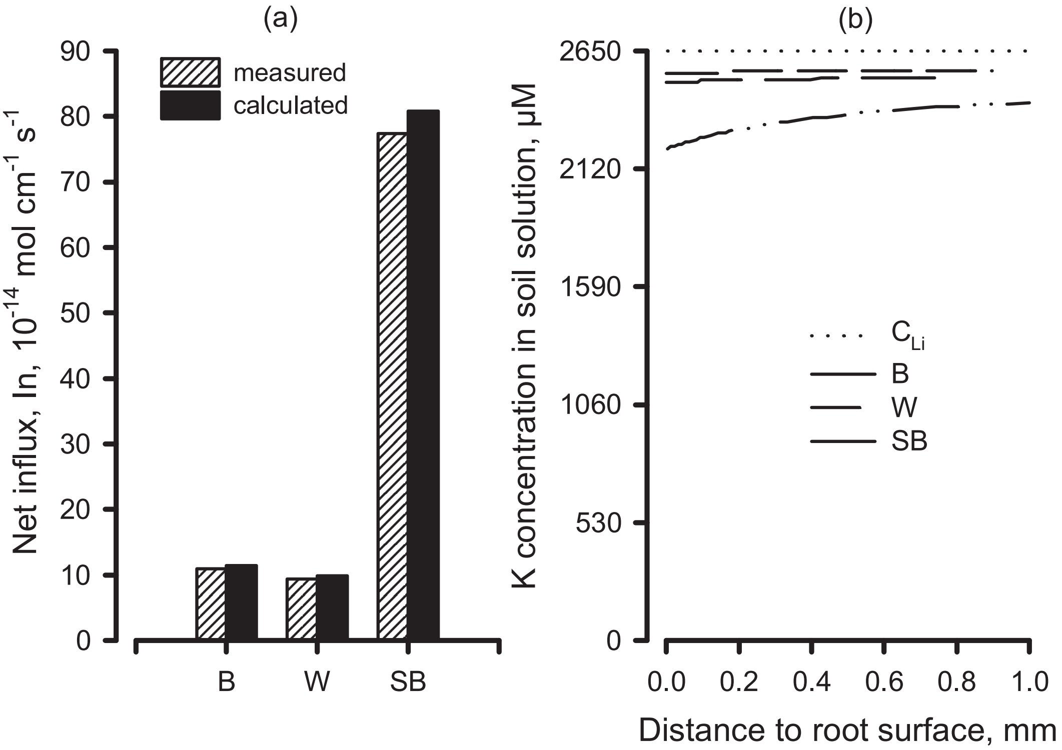

Fig. 3 *a) Comparison between measured and calculated K influx of barley (B), wheat (W) and sugar beet (SB) grown on a sandy clay loam at 2.65 mM soil solution K concentration. b) Calculated concentrations profiles of K in soil solution around the roots after 10 days of K uptake.*

Figure 4a shows that at a C_{Li} of 5 µM, K influx of both barley and wheat was over-predicted by the model by a factor of 3, whereas that of sugar beet was somewhat under-predicted. The model calculated around 76 % of the measured influx of sugar beet. Figure 4b shows the calculated concentration profiles around the roots of barley, wheat, and sugar beet at 5 µM, after the roots had absorbed K for 10 days. It can be seen, that barley and wheat decreased the K concentration from 5 µM in the bulk soil to about 2.5 µM at the root surface. In contrast sugar beet decreased the concentrations down to about 0.5 µM. This larger decrease caused a higher concentration difference (ΔC_L) between the bulk soil and the root surface, and is responsible for the higher calculated K influx of sugar beet as compared to the calculated influx of barley and wheat. For cereals, it is clear from figure 4b that K concentration at the root surface is not decreased to a minimum value, hence, transport was not the only problem but also the uptake kinetics. By sugar beet, the plant did more than expected and maximum transport was achieved. If we consider that the model describes the transport and uptake processes correctly, then some process more than just desorption, diffusion and mass flow as depicted in figure 1 (processes 1, 2 and 3, which are included in the model) took place.

For all 3 species the extension of the concentration profiles did not exceed 1 mm, indicating that the concentration profiles between neighbouring roots did not overlap and as such no inter-root competition for K existed (Fig. 4b).

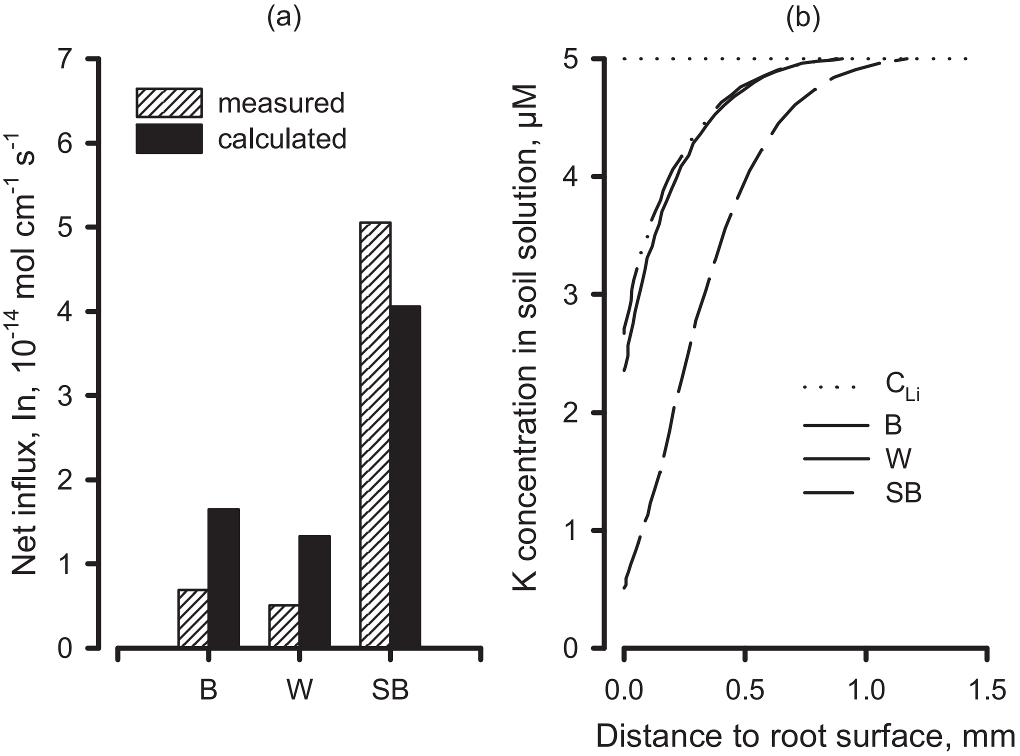

Fig. 4 *a) Comparison between measured and calculated K influx of barley (B), wheat (W) and sugar beet (SB) grown on a sandy clay loam at 5 µM soil solution K concentration. b) Calculated concentrations profiles of K in soil solution around the roots after 10 days of K uptake.*

The results show that depending on the plant species and K concentration in soil solution (C_{Li}), the model over-predicted, under-predicted and realistically predicted K uptake. The calculated concentration profiles around the roots are presented to try to explain the dynamics of K in the rhizosphere.

Field experiment

As in the pot experiment, under sufficient K conditions the model calculated correctly the measured uptake in the field of wheat and sugar beet (data not shown). It is more important to study the plant performance under deficient K conditions, hence, only the calculated uptake of plants from unfertilised treatments will be discussed here. The calculated K influx for sugar beet was drastically lower than measured, however, the degree of under-prediction of K influx by the model varied between the different growth periods (Fig. 5). Generally the model was able to calculate only 34 % of the actually measured uptake and the least calculated K influx was in the period June 24th -July 8th. It is interesting to note that it was at this growth period that the highest actual uptake occurred. On the other hand, calculated and measured K influx of wheat was more or less equal in the period May 27th -June 24th. In the period June 24th -July 8th, however, the model only calculated 40 % of the actual K influx (Fig. 5).

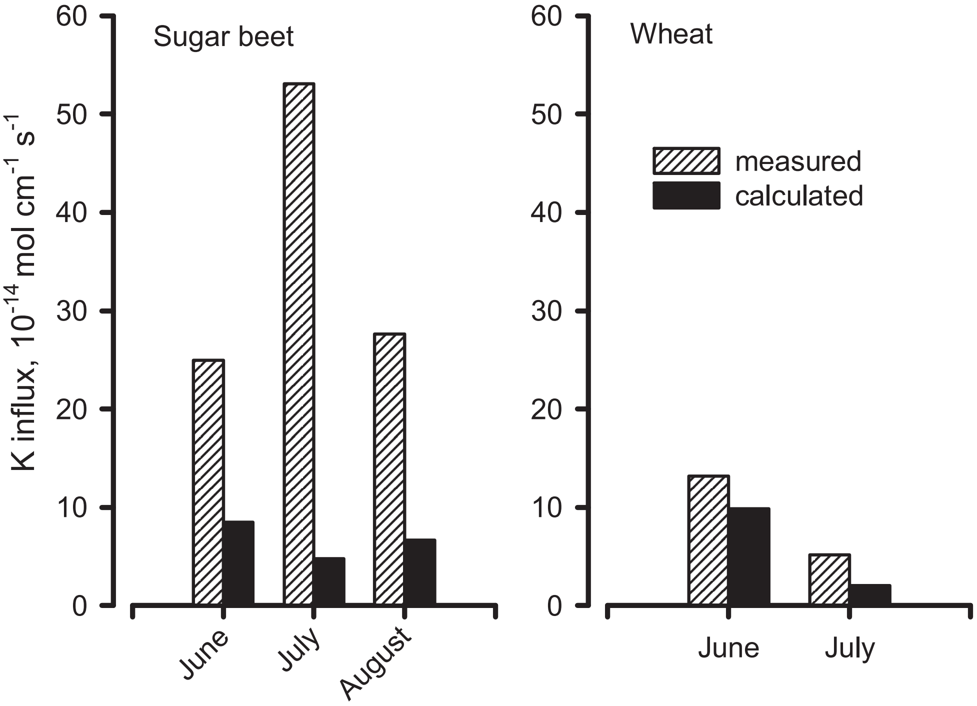

Fig. 5 *Comparison between measured and calculated K influx of wheat and sugar beet grown on a sandy clay loam in the field without K fertilisation.*

Figure 6 shows the concentration profiles around the roots of sugar beet and wheat grown in the field without K fertilisation in the 0-15 cm layer in the period June 24th to July 8th. Both plant species decreased the concentration at the root surface to around 0.5 µM, which corresponded to 12 and 22 % of the C_{Li} of sugar beet and wheat, respectively. The respective resulting ΔC_L were 4 and 2 µM. No root competition existed, since the concentration at r_1 reached the value of C_{Li}.

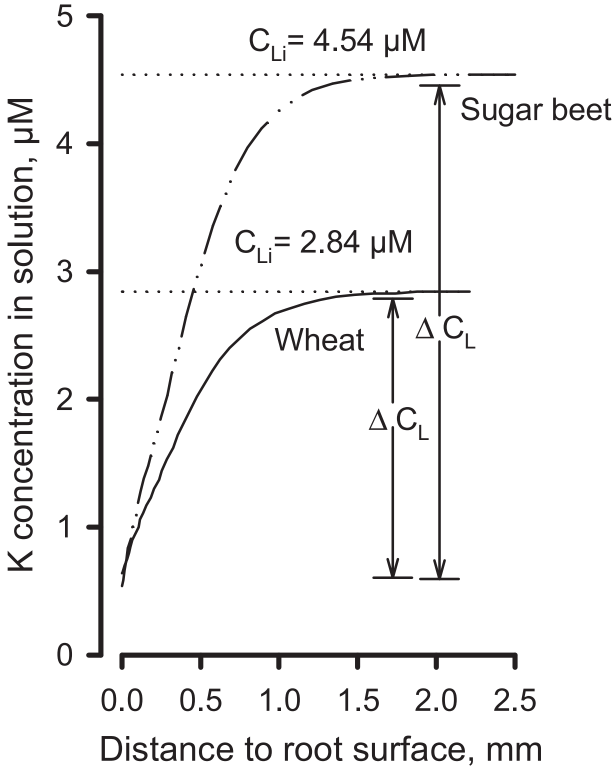

Fig. 6 *Calculated concentrations profiles of K in soil solution around the roots of sugar beet and wheat grown on a sandy clay loam soil in the field in the period June* 24th- July 8th.

Sensitivity analysis

For modelling K influx different soil and plant parameters were used. Some of these parameters could be easily and accurately measured, for example, Θ, whereas others such as I_{max} are not easily and accurately obtainable for plants grown in soil. To quantify the influence of the different parameters used in the model on the calculated K influx and uptake, and to find out whether a possibly wrong used parameters could explain the discrepancy between calculated and measured K uptake, a sensitivity analysis was carried out. Each time only one parameter is changed while all other inputs are kept constant. The soil parameters used in the sensitivity analysis in the pot experiment were C_{Li} and b. The physiological uptake parameters were not measured in this study, and I_{max} was chosen to study the effect of the root uptake capacity on K uptake.

Figure 7 shows the effect of varying different soil and plant parameters on the K influx of wheat and sugar beet, grown under controlled conditions at a C_{Li} of 5 µM. It is obvious that C_{Li} had the strongest influence on K influx, where doubling C_{Li} doubled the calculated influx of both species. The calculated influx of wheat increased with increasing I_{max}, whereas that of sugar beet remained practically unchanged.

As could be seen from the concentration profiles presented in figure 4b, wheat decreased the concentration at the root surface (C_{Lo}) by far less than sugar beet, a further decrease of C_{L0} would increase ΔC_L and, consequently, the concentration gradient and the diffusive flux to the roots and thereby the influx. This could be achieved by higher uptake capacity of the root and thus increasing I_{max} increased calculated K influx of wheat. Sugar beet had established the maximum ΔC_L by decreasing C_{L0} to nearly C_{Lmin}, hence, the maximum transport to roots is established and increasing I_{max} would not enhance K influx. Increasing buffer power (b) did not have a great influence on calculated K influx where doubling b value increased calculated influx of wheat and sugar beet just by 11 % and 13 %, respectively, (Fig. 7).

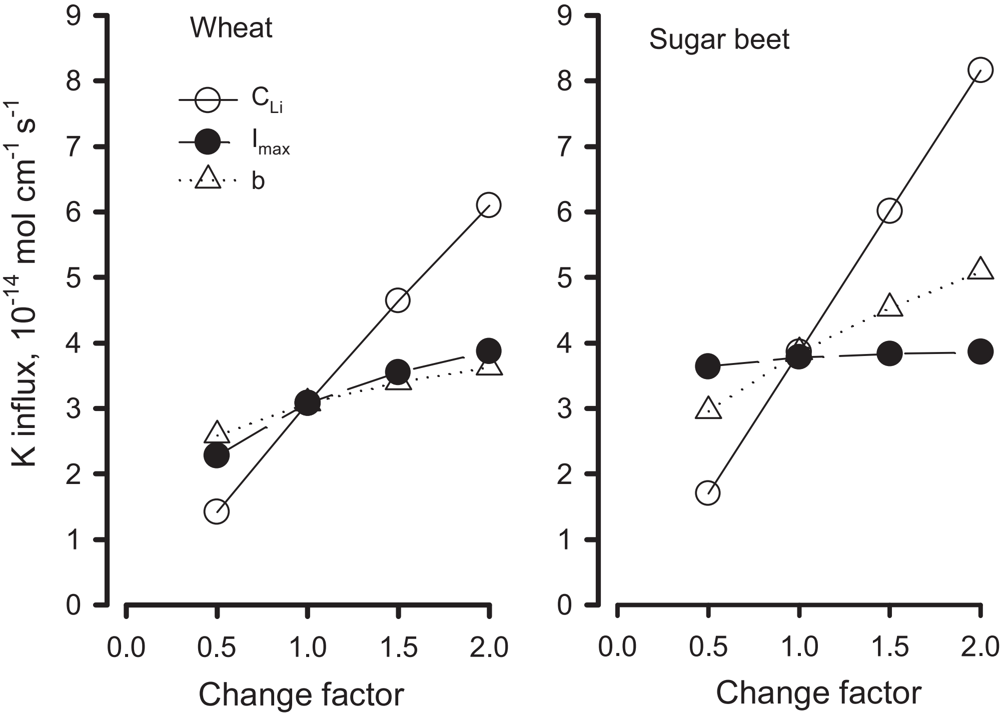

Fig. 7 *Sensitivity analysis for sugar beet and wheat grown under controlled conditions at 5 µM K soil solution concentration.*

The effect of b found in this study was greater than that reported by Claassen (1994) who found that increasing b by factor 10 brought a negligible increase in calculated K influx when no root competition for K existed. The author simulated K uptake without taking uptake by root hairs into account, and the simulation in this study included uptake by root hairs, and among them existed competition for K.

Buffer power influences calculated K uptake only if root competition existed (Claassen, 1994). Claassen and Steingrobe (1999) explained that, since diffusion occurs in the liquid phase, then it is the gradient in solution ($\Delta C_L/\Delta x$) rather than the gradient of available nutrients ($\Delta C/\Delta x$) which is the deciding factor for diffusion. Since the relation between both gradients is described by the buffer power, the authors calculated F_D in terms of the gradient in solution as $-D_L\ \Theta f\ \Delta C_L/\Delta x$. As such b would have an influence on F_D by its effect on Δx, but under cylindrical geometry as found around roots this effect seems small. Since buffer power describes the available nutrients at a given soil solution concentration, then the amount of available nutrient is more in a high buffering soil, and competition for nutrients will be later than in a low buffering soil.

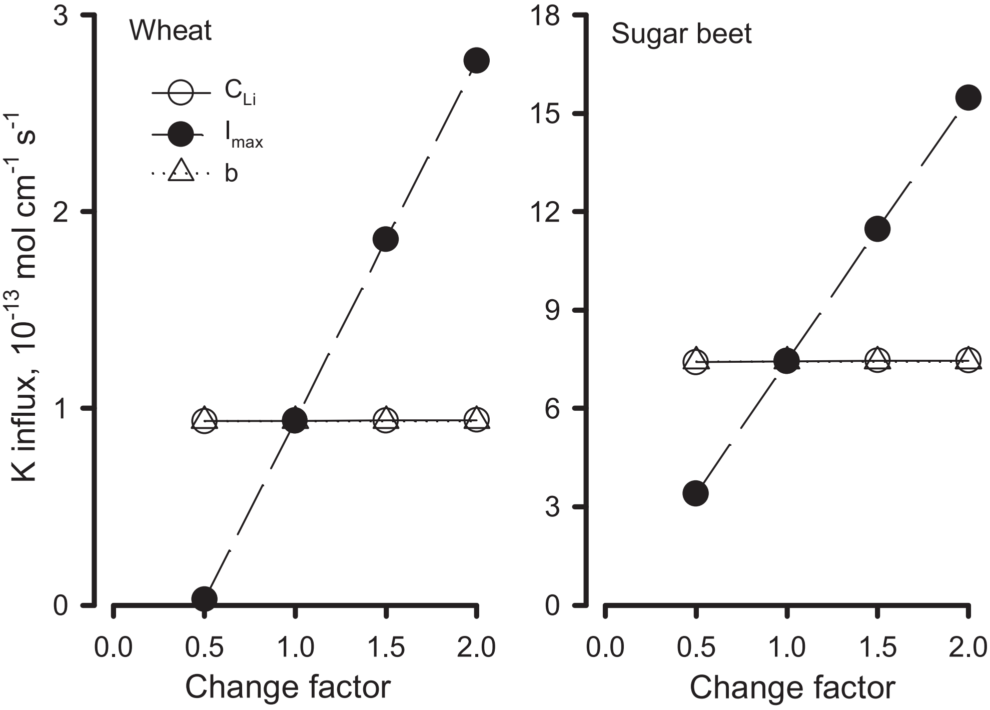

Fig. 8 *Sensitivity analysis for sugar beet and wheat grown under controlled conditions at a high K soil solution concentration of 2.65 mM.*

The results of the sensitivity analysis for wheat and sugar beet at a C_{Li} of 2.65 mM are shown in figure 8. Here the situation is completely reversed, where it is obvious that under conditions of high soil solution concentration, increasing C_{Li} and/or b has absolutely no influence on the calculated K influx. Hence, only an increased root uptake capacity, for example, I_{max} would enhance the influx.

Figure 9 shows the results of the sensitivity analysis conducted for sugar beet and wheat grown in the field in the period June 24th -July 8th. As is seen, under these conditions, and for both crops, only a higher C_{Li} value would be effective in covering the gap between the calculated and measured influx.

The influence of C_{Li} on calculated influx was similar for the two plant species, however, for sugar beet the discrepancy between measured and calculated influx was much higher. Hence, doubling C_{Li} value for wheat was enough to equalise calculated and measured influx, whereas the C_{Li} value for sugar beet had to be increased by factor 10 in order to achieve the same effect. An increased I_{max} or b would not improve the calculated uptake, as is seen, even by increasing both parameters by factor 10, the calculated influx was not equal to measured. This is because both species created the highest possible ΔC_L (Fig. 6) and as such maximum diffusive flux to the roots, a higher I_{max} or b value would not influence calculated uptake.

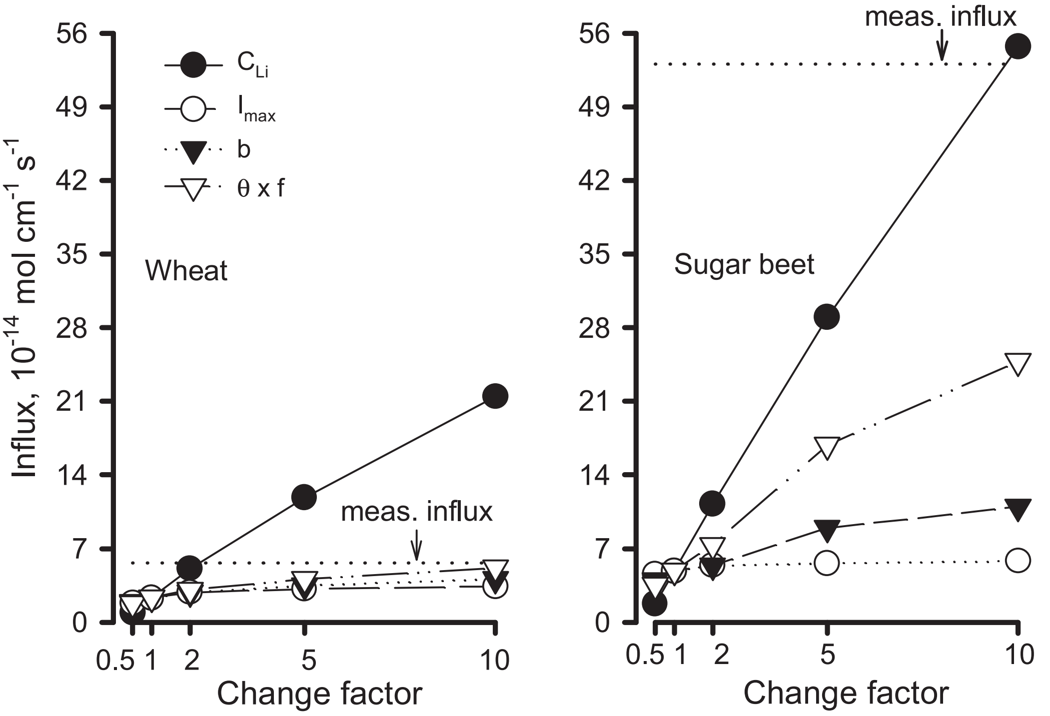

Fig. 9 *Sensitivity analysis for sugar beet and wheat grown on a sandy clay loam in the field in the growth period June 24th -July.8th.*

The diffusion path is through water-filled pores only, hence, Θ affects both the diffusion path and the diffusion cross-sectional area. At high volumetric water content (Θ), the diffusion path will be more direct than under low Θ conditions, where the ions will pass through a longer and more tortuous path, that is they will be met with higher resistance. This resistance is described by the impedance factor (f), where f is the inverse of the resistance. The combined influence of Θ x f on the calculated K uptake is evaluated, since changing Θ changes f, and the relation between both factors is nearly linear in the range of available water (Bhadoria et al., 1991). Since Θ and f describe the nature of the diffusion path, it is expected to be very influential on calculated K uptake. Influence of Θ x f on calculated K uptake although greater than the influence of I_{max} and b was, however, by far lower than that of C_{Li}. Increasing Θ x f by factor 10 helped to explain the discrepancy between calculated and measured influx for wheat, whereas that increased calculated uptake of sugar beet by 50 % (Fig. 9). In a dry soil the diffusion coefficient (D_e) is small and the plant needs steeper gradients in order to increase the flux to the roots. This is possible through the smaller extension of the depletion zones in dry as compared to wet soil (Fig. 10).

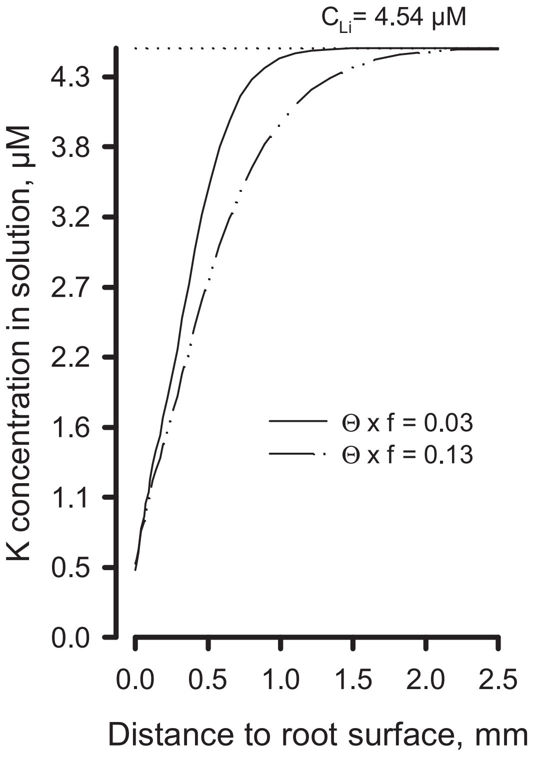

Fig. 10 *Concentration profiles around the roots of sugar beet on a sandy clay loam in the field at low and high Θ x f conditions.*

However, in dry soils nutrient mobility is by far much reduced resulting in low flux to the roots and accordingly uptake per unit root. Hence, the roots would not be able to improve the low transport encountered under dry soil conditions by decreasing C_{L0} to a lower value. Using $F_D = -D_e \cdot \frac{dC}{dx}$ and $D_e = D_L \Theta f \frac{\Delta C}{\Delta x}$ and for the extension of the depletion zones $\Delta x = \sqrt{\pi D_e t}$, it can be shown that F_D is proportional to $\sqrt{\Theta f}$. This explains also the non linear function of Θ x f to the flux in comparison to the linear relation found between the soil solution concentration (C_{Li}) and the diffusion flux, since $D_e = D_L \Theta f \frac{\Delta C}{\Delta x}$.

Discussion

Nutrient availability in soil and plants ability to acquire nutrients are the basis for supplying plants with mineral nutrients (Jungk and Claassen, 1997). Therefore, both soil and plant properties are important for plant nutrition. Nutrient availability encompasses the chemically available nutrients and their movement in soil. The acquiring ability of plants is characterised by the size of the root system and by morphological root properties such as root length, root radius (r_0) and root hairs, and physiological properties such as the uptake parameters (I_{max}, K_m, and C_{Lmin}) and exudation of solubilising compounds, which in turn determine the uptake rate per unit root and time.

Several authors reported similar calculated K uptake by the model as measured by different plant species, grown under various K conditions (Silberbush and Barber, 1984; Claassen 1994; Steingrobe and Claassen, 2000). In this study, K uptake was calculated realistically by the model in some cases, in others, calculated K uptake was either over- or under-predicted by the model.

In the pot experiment at the highest fertilisation level with a C_{Li} of around 2.65 mM, the model simulated the measured uptake accurately (Fig. 3a). As shown by the larger extension of the depletion zones due to the smaller b value (Fig. 3b), the C_{Li} was depleted over the whole soil volume. Kuchenbuch (1983) explained that the geometrically radial form of the concentration profiles around single roots increases the spatial access to larger K amounts from the exchangeable fraction.

At 5 µM soil solution K concentration, the model was unable to estimate the measured K influx of all 3 plant species. For the cereals, the calculated as compared to measured uptake, was nearly 3 times higher at this low C_{Li} value. Since the concentration profiles showed that both plant species did not decrease the C_{L0} to minimum values and thus the maximum concentration difference was not established, indicating low transport to the roots (Fig. 4b). A further decrease of C_{L0} caused by higher I_{max} values would have resulted in a higher ΔC_L, which would have meant steeper concentration gradients and as such an even higher K flux to the roots.

The sensitivity analysis had shown that at a C_{Li} of 5 µM, I_{max} had a greater influence on calculated K uptake of wheat (Fig. 7). So discrepancy between calculated and measured uptake could have been because of an actually much lower I_{max} value of the plant than that used in the model calculation. Steingrobe and Claassen (2000) modelled the K influx of wheat, grown in a similar soil, and suggested that, since the maximum possible ΔC_L was not established by wheat, a higher flux to the roots would have been obtained by increasing I_{max}. The authors attributed the over-prediction of the influx to a wrong estimate of I_{max}. Since I_{max} is not directly measurable in soil, a correct input value is not available. It remains to be answered why K deficient plants were not able to increase I_{max}, since as was seen by K fertilised plants higher I_{max} values could be established.

To achieve the much higher measured influx as compared to the cereals, sugar beet needed a much greater ΔC_L. This was possible by decreasing the concentration at the root surface further (down to 0.5 µM) than the cereals. The resulting concentration gradients were steeper and also maximum K flux to the roots was achieved (Fig. 4b). Hence, increased uptake capacity of the roots such as higher I_{max} did not enhance uptake, since it was K transport that limited uptake.

The sensitivity analysis showed that under K deficiency conditions, only an increase in the C_{Li} could bridge the gap between measured and calculated influx. According to Steingrobe and Claassen (2000) and Claassen (1994) the higher the C_{Li} the greater is the possible concentration difference (ΔC_L) between the bulk soil and the root surface, and if transport capacity of the soil limits influx, the plant would be able to reduce the concentration at the root surface to nearly zero, consequently, ΔC_L depends only on C_{Li}, therefore, flux towards the roots and, hence, influx is closely related to C_{Li}. From this it could be concluded that higher calculated influx could be achieved only by using a higher value for C_{Li} in modelling.

The results of the pot experiment, showed that the cereals had a large root system and accordingly a smaller needed influx, that was covered by the transport in soil and the root physiology. Hence, the model described the uptake correctly. On the other hand, sugar beet had a higher influx which could only be explained by the model by using higher C_{Li} values. The concentration in soil solution is a parameter which can be measured fairly accurately and the use of an incorrect C_{Li} value in the model is rather unlikely. This indicates that some processes which increase C_{Li} occur in the rhizosphere. These processes are not included in the model and their nature is not known.

In the field experiment, calculated K uptake of wheat was only realistically estimated by the model in the period May 27th -June 24th (Fig. 5). It seems that the ΔC_L created was enough to provide the necessary concentration gradient needed to drive nearly the actually measured K flux to the roots. However, calculated K uptake was under-predicted by nearly 50 %, in the period June 24th -July 8th (Fig. 5), and was drastically under-predicted for sugar beet, especially in July, the time of highest K requirement (Fig. 5). The results contrast with those of Claassen (1994), who found similar calculated and measured K uptake by sugar beet, with and without fertilisation and under-prediction of K uptake for wheat in July, in the unfertilised treatments only. Both crops decreased the C_{L0} to around 0.5 µM, as was shown by the concentration profiles around the roots of wheat and sugar beet in the period June 24th -July 8th (Fig. 6). Due to the higher C_{Li} on sugar beet plots, a higher ΔC_L was possible and, consequently, steeper concentration gradients and higher diffusive transport to the roots. Hence, sugar beet was able to achieve a higher influx in comparison to wheat. Nevertheless, as is seen in figure 5, the calculated influx of sugar beet, in the period 24.6 - 8.7, was somewhat lower than that of wheat. The calculated uptake was obtained by summing up the uptake from the single soil layers (0-90 cm). The soil solution concentration at the 15-30 cm was very low (1.43 µM), consequently, the calculated uptake in this layer was also low and, hence, the observed discrepancy, since figure 6 represents only the calculated concentration profiles in the soil layer 0-15 cm. It is interesting to note that in July, the period of highest demand for K, and although C_{Li} and ΔC_L were lower than in June, nevertheless, the actual uptake was highest, whereas the model calculated the least (9 %) uptake (Fig. 5).

The reasons for the large discrepancy between calculated and measured K influx could not be attributed to an incorrect determination of input parameters. As was shown in the sensitivity analysis (Fig. 9), for sugar beet, only increasing the soil solution concentration (C_{Li}) could explain the discrepancy between measured and calculated influx. For wheat, the gap between measured and calculated influx could be bridged by a higher C_{Li} or else by a higher Θ x f. It is obvious that K transport was the limiting factor for uptake. As such although Θ had a greater influence on calculated uptake, since it influences mainly (D_e), and the values of Θ varied greatly during the different growth periods (0.36-0.44), but higher Θ values, at least for sugar beet, did not cover the discrepancy between observed and calculated influx. For wheat, a factor 10 increase of Θ x f increased calculated K influx to a value similar to that measured (Fig. 9), however, such a large increase is not realistic.

Concentration in soil solution can be measured relatively accurately and as such it is least possible that the values used in the modelling are incorrect. For wheat, doubling the C_{Li} was enough to cover the observed discrepancy between measured and calculated influx, whereas for sugar beet a 10 times higher C_{Li} was needed (Fig. 9). If we assume, which is most unlikely, that incorrectly only half the soil solution K concentration was measured in the case of wheat, it would be impossible, indeed, to assume that only one tenth of the actual C_{Li} was measured for sugar beet. Hence, a wrong C_{Li} could not be the reason to explain the observed discrepancy.

The root physiological characteristics or the uptake kinetics (I_{max}, K_m, and C_{lmin}) were not measured directly in the soil, as such the probability of inaccuracy is much higher by those factors. Claassen (1994) attributed the reduced K uptake by sugar beet in June to a very high K_m value, since the plants, even under K deficiency conditions, were unable to further decrease the concentrations at the root surface and, therefore, increase the K flux to root. However, as was discussed in the pot experiment, when transport in the soil is limiting uptake, improving K uptake kinetics such as increasing I_{max} or decreasing K_m and C_{Lmin} would not help in increasing calculated potassium uptake. Especially for sugar beet, where the sensitivity analysis showed that increasing I_{max} by factor 10 increased calculated K uptake only by 11% (Fig. 9). In the case of wheat, in the period June 24th -July 8th, a further decrease of C_{L0} to minimum concentrations, and taking into consideration that increasing I_{max} has a somewhat higher effect on calculated K uptake of wheat (Fig. 9), would not be enough to explain a difference of 50 % between calculated and measured uptake. The reason for the observed discrepancy between measured and calculated uptake could be due to the fact that the model describes only sorption and transport of nutrients in the soil as well as uptake. However, it seems that the plants did influence the rhizosphere chemically, thereby increasing the nutrient availability. The increased nutrients availability had a similar effect to that of an increased C_{Li} in the model. The source of the larger amount of available K may be the non-exchangeable K. Meyer and Jungk (1993) explained the discrepancy between measured and calculated uptake by including the release kinetics of the non-exchangeable K in the model. Whether the release of non-exchangeable K is due to some root exudates such as organic acids or protons which exchange for K, or some other phenomena is not known.

An interesting observation is that the plants in the field were able to achieve a much higher influx as compared to those grown under controlled conditions. Evidence exists that plant roots cause acidification in the rhizosphere by light dependent active excretion of H^+ (Mengel and Malissiovas, 1982). Hence, the higher light intensity in the field, as compared to the growth chamber, could be the reason for the higher K influx of plants grown in the field. The excreted H^+, probably accompanied by the release of organic anions, must be of vital significance for many reactions going on in the rhizosphere.

In contrast to the role played by organic acids in mobilising phosphate and micronutrients (Gerke, 1993; Cakmak et al., 1994; Rengel et al., 1998; Beißner and Römer, 1998), very little information is available on the role played by organic acids on K mobilisation in the rhizoshere. Citric acid, added in a quantity analysed in the rhizosphere of the proteoid roots of white lupine, is reported to increase the amount of electro-ultrafiltration (EUF) extractable non-exchangeable K of the soil (Steffens and Zarhoul, 1997). The plants exude ions, for example, protons in the rhizosphere which lead to higher release of non-exchangeable K (Kuchenbuch, 1983). However, Springob and Richter (1998) showed that additional proton induced release of non-exchangeable K is negligible above pH 4, hence, it might be that not only exuded substances by the roots lead to increasing the availability of K in the rhizosphere.

Evidence also exists that a decrease of the soil solution concentration to 2-3 µM initiates release of non-exchangeable K (Claassen et al., 1981; Springob and Richter, 1998). The latter reported a six times higher K release rate at 3 µM than at 4 µM and suggested that a further decrease of only 1 µM K, achieved may be through intensive K uptake by the plants, would make it possible to access to considerable K reserves within a short time.

Conclusions

1. At high soil solution concentration, transport by mass flow and diffusion was not limiting uptake and K influx was determined by I_{max}.
2. The correct prediction of the measured uptake of wheat by the model means that its large root system and accordingly the smaller needed influx were the reason for its K efficiency.
3. The model was not able to describe the uptake under K deficiency conditions. This leads to the conclusion that some processes which increase the availability of nutrients occur in the rhizosphere. This higher nutrient availability can be obtained by the model only by an increased C_{Li}.
4. These processes might have played a central role by the generally higher influx of sugar beet.

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Appendix

Table 5.1 *Soil and plant parameters used for calculating K uptake of wheat at different fertilisation levels between 1st and 2nd harvest*

	Fertilisation g K kg^{-1} soil	
	0	2.4
C_{Li}, mol cm^{-3}	5.03×10^{-9}	2.65×10^{-6}
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98
Θ, cm^3 cm^{-2}	0.36	0.36
f	0.16	0.16
v_0, 10^{-7} cm^3 cm^{-2}	4.61	1.85
b	1268	32
I_{max}, 10^{-12} mol cm^{-2} s^{-1}	4.01	1.30
K_m, 10^{-9} mol cm^{-3}	9.7	9.7
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00
r_0, 10^{-3} cm	8.0	7.0
r_1, cm	0.16	0.10
RL_0, cm	19271	38065
k, d^{-1}	0.055	0.11

Table 5.2 *Parameters of wheat root hairs used for calculating K uptake at different fertilisation levels between 1st and 2nd harvest*

Distance from root	Wheat	
	N (1)	r_1h (2)
cm		10^{-3} cm
0.000-0.025	720	11.3
0.025-0.050	140	33.2
0.050-0.075	50	62.2
0.075-0.100	30	90.6
0.100-0.125	20	160.0
Total length (cm cm^{-1} root)	15	
average length (cm)		0.021

(1) *N = number of root hairs per cm root.*

(2) *r_1h =half average distance between neighbouring root hairs.*
1 and 2 from Claassen (1994).

Table 5.3 *Soil and plant parameters used for calculating K uptake of barley at different fertilisation levels between 1st and 2nd harvest*

	Fertilisation g K kg^{-1} soil	
	0	2.4
C_{Li}, mol cm^{-3}	5.03×10^{-9}	2.65×10^{-6}
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98
Θ, cm^3 cm^{-2}	0.34	0.34
f	0.16	0.16
v_0, 10^{-7} cm^3 cm^{-2}	3.48	1.30
b	1393	33
I_{max}, 10^{-12} mol cm^{-2} s^{-1}	5.12	1.37
K_m, 10^{-9} mol cm^{-3}	9.7	9.7
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00
r_0, 10^{-3} cm	8.0	8.0
r_1, cm	0.15	0.09
RL_0, cm	23749	48942
k, d^{-1}	0.057	0.10

Table 5.4 *Parameters of barley root hairs used for calculating K uptake at different fertilisation levels at 1st and 2nd harvests*

Distance from root	Barley	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	1000	9.16
0.025-0.050	310	22.1
0.050-0.075	120	41.5
0.075-0.100	60	71.6
0.100-0.125	20	160.0
Total length (cm cm^{-1} root)	25	
average length (cm)		0.025

(1) *N = number of root hairs per cm root.*

(2) *r_1h =half average distance between neighbouring root hairs.*

1 and 2 from Claassen (1994).

Table 5.5 *Soil and plant parameters used for calculating K uptake of sugar beet at different fertilisation levels between 1st and 2nd harvest*

	Fertilisation g K kg^{-1} soil	
	0	2.4
C_{Li}, mol cm^{-3}	5.03×10^{-9}	2.65×10^{-6}
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98
Θ, cm^3 cm^{-2}	0.36	0.36
f	0.16	0.16
v_0, 10^{-7} cm^3 cm^{-2}	4.41	4.67
b	1035	31
I_{max}, 10^{-12} mol cm^{-2} s^{-1}	59.9	8.91
K_m, 10^{-9} mol cm^{-3}	3.60	6.60
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00
r_0, 10^{-3} cm	6.0	9.73
r_1, cm	0.26	0.19
RL_0, cm	7710	11805
k, d^{-1}	0.05	0.10

Table 5.6 *Parameters of sugar beet root hairs used for calculating K uptake at different fertilisation levels between 1st and 2nd harvests*

Distance from root	Sugar beet	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	560	13.3
0.025-0.050	130	40.9
0.050-0.075	30	284.0
0.075-0.100	10	650.0
Total length (cm cm^{-1} root)	11	
average length (cm)		0.020

(1) *N = number of root hairs per cm root.*

(2) *r_1h =half average distance between neighbouring root hairs.*
1 and 2 from Claassen (1994).

Table 5.7 *Soil and plant parameters used for calculating K uptake of wheat in the field without fertilisation at 0-15 cm soil depth*

	Time	
	May 27th -June	June 24th -July 8th
C_{Li}, 10^{-9} mol cm^{-3}	6.45	2.84
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98
Θ, cm^3 cm^{-2}	0.35	0.40
f	0.17	0.22
v_0, 10^{-7} cm^3 cm^{-2}	7.14	4.76
b	1569	1569
I_{max}, 10^{-12} mol cm^{-2} s^{-1}	2.43	4.13
K_m, 10^{-9} mol cm^{-3}	9.7	9.7
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00
r_0, 10^{-2} cm	1.40	1.20
r_1, cm	0.28	0.25
RL_0, cm	514934	713174
k, cm m^{-2} d^{-1}	6723	7809

Table 5.8 *Parameters of wheat root hairs used for calculating K uptake in the field without fertilisation (0-15 cm)*

Distance from root	Wheat	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	720	11.3
0.025-0.050	140	33.2
0.050-0.075	50	62.2
0.075-0.100	30	90.6
0.100-0.125	20	160.0
Total length (cm cm^{-1} root)	15	
average length (cm)		0.021

(1) *N = number of root hairs per cm root.*

(2) *r_1h =half average distance between neighbouring root hairs.*
1 and 2 from Claassen (1994).

Table 5.9 *Soil and plant parameters used for calculating K uptake of wheat in the field without fertilisation at 15-30 cm soil depth*

	Time	
	May 27th -June	June 24th -July 8th
C_{Li}, 10^{-9} mol cm^{-3}	3.63	2.19
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98
Θ, cm^3 cm^{-2}	0.37	0.39
f	0.18	0.21
v_0, 10^{-7} cm^3 cm^{-2}	7.14	4.76
b	1569	1569
I_{max}, 10^{-12} mol cm^{-2} s^{-1}	3.40	6.26
K_m, 10^{-9} mol cm^{-3}	9.70	9.70
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00
r_0, 10^{-3} cm	10.0	8.00
r_1, cm	0.33	0.30
RL_0, cm	392168	510841
k, cm m^{-2} d^{-1}	4238	5237

Table 5.10 *Parameters of wheat root hairs used for calculating K uptake in the field without fertilisation (15-30 cm)*

Distance from root	Wheat	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	720	11.3
0.025-0.050	140	33.2
0.050-0.075	50	62.2
0.075-0.100	30	90.6
0.100-0.125	20	160.0
Total length (cm cm^{-1} root)	15	
average length (cm)		0.021

(1) N = *number of root hairs per cm root.*

(2) *r_1h =half average distance between neighbouring root hairs.*

1 and 2 from Claassen (1994).

Table 5.11 *Soil and plant parameters used for calculating K uptake of wheat in the field without fertilisation at 30-60 and 60-90 cm soil depth*

	Time	
	June 24th -July 8th	June 24th -July 8th
	30-60 cm	60-90 cm
C_{Li}, 10^{-9} mol cm^{-3}	2.56	5.40
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98
Θ, cm^3 cm^{-2}	0.42	0.41
f	0.24	0.21
v_0, 10^{-7} cm^3 cm^{-2}	4.76	4.76
b	1569	1569
I_{max}, 10^{-12} mol cm^{-2} s^{-1}	4.76	2.20
K_m, 10^{-9} mol cm^{-3}	9.70	9.70
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00
r_0, 10^{-2} cm	1.10	2.33
r_1, cm	0.49	0.94
RL_0, cm	386712	0.00
k, cm m^{-2} d^{-1}	1034	7664

Table 5.12 *Parameters of wheat root hairs used for calculating K uptake in the field without fertilisation (30-60, 60-90 cm)*

Distance from root	Wheat	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	720	11.3
0.025-0.050	140	33.2
0.050-0.075	50	62.2
0.075-0.100	30	90.6
0.100-0.125	20	160.0
Total length (cm cm^{-1} root)	15	
average length (cm)		0.021

(1) *N = number of root hairs per cm root.*

(2) *r_1h =half average distance between neighbouring root hairs.*

1 and 2 from Claassen (1994).

Table 5.13 *Soil and plant parameters used for calculating K uptake of sugar beet in the field without fertilisation at 0-15 cm soil depth*

	Time		
	May 27th -June	June 24th -July 8th	July 8th -Aug. 5th
C_{Li}, 10^{-9} mol cm^{-3}	10.4	4.54	4.06
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98	1.98
Θ, cm^3 cm^{-2}	0.40	0.36	0.40
f	0.22	0.18	0.22
v_0, 10^{-7} cm^3 cm^{-2}	2.35	1.45	1.01
b	1114	1114	1114
I_{max}, 10^{-11} mol cm^{-2} s^{-1}	1.68	2.19	2.81
K_m, 10^{-9} mol cm^{-3}	6.60	6.60	6.60
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00	5.00
r_0, 10^{-3} cm	10.0	9.33	10.2
r_1, cm	0.33	0.41	0.36
RL_0, cm	210918	249200	313984
k, cm m^{-2} d^{-1}	1367	4627	4250

Table 5.14 *Parameters of sugar beet root hairs used for calculating K uptake in the field without fertilisation (0-15 cm)*

Distance from root	Sugar beet	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	560	13.3
0.025-0.050	130	40.9
0.050-0.075	30	284.0
0.075-0.100	10	650.0
Total length (cm cm^{-1} root)	11	
average length (cm)		0.020

(1)N = number of root hairs per cm root.

(2) *r_1h = half average distance between neighbouring root hairs.*

1 and 2 from Claassen (1994).

Table 5.15 *Soil and plant parameters used for calculating K uptake of sugar beet in the field without fertilisation at 15-30 cm soil depth*

	Time		
	May 27th - June	June 24th -July 8th	July 8th -Aug. 5th
C_{Li}, 10^{-9} mol cm^{-3}	9.98	1.43	5.13
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98	1.98
Θ, cm^3 cm^{-2}	0.42	0.42	0.42
f	0.24	0.24	0.24
v_0, 10^{-6} cm^3 cm^{-2}	2.35	1.45	0.83
b	1114	1114	1114
I_{max}, 10^{-11} mol cm^{-2} s^{-1}	1.44	4.02	2.83
K_m, 10^{-9} mol cm^{-3}	6.60	6.60	6.60
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00	5.00
r_0, 10^{-3} cm	8.65	9.34	10.2
r_1, cm	0.51	0.45	0.41
RL_0, cm	165449	211585	252751
k, cm m^{-2} d^{-1}	1648	2940	2025

Table 5.16 *Parameters of sugar beet root hairs used for calculating K uptake in the field without fertilisation (15-30 cm)*

Distance from root	Sugar beet	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	560	13.3
0.025-0.050	130	40.9
0.050-0.075	30	284.0
0.075-0.100	10	650.0
Total length (cm cm^{-1} root)	11	
average length (cm)		0.020

(1)N = number of root hairs per cm root.

(2) *r_1h =half average distance between neighbouring root hairs.*
1 and 2 from Claassen (1994).

Table 5.17 *Soil and plant parameters used for calculating K uptake of sugar beet in the field without fertilisation at (30-60, 60-90) cm soil depth*

	Time		
	May 27th -June	June 24th -July 8th	July 8th -Aug. 5th
	30-60 cm		60-90 cm
C_{Li}, 10^{-9} mol cm^{-3}	1.79	2.54	2.89
D_L, 10^{-5} cm^2 s^{-1}.	1.98	1.98	1.98
Θ, cm^3 cm^{-2}	0.40	0.43	0.41
f	0.22	0.22	0.22
v_0, 10^{-6} cm^3 cm^{-2}	1.45	1.01	1.01
b	1114	1114	1114
I_{max}, 10^{-11} mol cm^{-2} s^{-1}	1.59	0.73	0.52
K_m, 10^{-9} mol cm^{-3}	6.60	6.60	6.60
C_{Lmin}, 10^{-10} mol cm^{-3}	5.00	5.00	5.00
r_0, 10^{-2} cm	1.30	1.00	1.60
r_1, cm	0.93	0.76	1.13
RL_0, cm	99754	120617	0.00
k, cm m^{-2} d^{-1}	1490	4149	2691

Table 5.18 *Parameters of sugar beet root hairs used for calculating K uptake in the field without fertilisation (30-60, 60-90) cm*

Distance from root	Sugar beet	
cm	N (1)	r_1h (2) 10^{-3} cm
0.000-0.025	560	13.3
0.025-0.050	130	40.9
0.050-0.075	30	284.0
0.075-0.100	10	650.0
Total length (cm cm^{-1} root)	11	
average length (cm)		0.020

(1)N =number of root hairs per cm root.

(2) *r_1h =half average distance between neighbouring root hairs.*

1 and 2 from Claassen (1994).

Chapter 6

Effect of Citric and Malic Acid on the Release of Interlayer Bound K of a Sandy Clay Loam

Abstract

In the last chapter, K uptake of various plant species, both under controlled and field conditions, was simulated by a mechanistic model. The results showed that under deficient K conditions, the model was unable to predict actually measured K influx. Moreover, sensitivity analysis revealed that the gap between calculated and measured influx could only be bridged by increasing the K concentration in soil solution. This indicates that some processes, which were not considered by the model, occur in the rhizosphere and lead to increased C_{Li}. One such process could be the K chemical mobilisation by root exudates.

With the objective to study the influence of root exudates, as measured in stressed white lupine plants, on interlayer K release, the sandy clay loam soil, used throughout this study, was desorbed for 72 hours, using different concentrations of citric and malic acid in 0.01 M $CaCl_2$ (Ca^{++} concentrations measured in the soil solution).

The study showed that citric acid significantly enhanced interlayer K release from a sandy clay loam as compared to malic acid and $CaCl_2$ (control). Desorption by malic acid, on the other hand, did not release higher K amounts than the control.

Research under natural conditions is necessary to quantify interlayer K release by root exudates.

Introduction

Results of the previous chapter, showed that a nutrient simulation model (Claassen, 1994) strongly under-predicted K uptake of different plant species grown on a "K fixing" sandy clay loam soil, under controlled conditions and in the field. The model assumes K transport to roots only by mass flow and diffusion. It does not take into consideration the chemical changes caused by the roots in the rhizosphere. The sensitivity analysis showed that the observed influx of these species could only be achieved by increasing the K concentration in the soil solution (C_{Li}). This is a fairly accurately measured parameter and as such the use of an incorrect value, for simulating the K uptake, could not be an acceptable explanation. Accordingly chemical mobilisation of K in the rhizosphere by plant root was suggested as a possible cause for the higher observed K influx.

Many reports showed that the chemical mobilisation of mineral nutrients in the rhizosphere by plant roots, can play a decisive role in the mobilisation and acquisition of both anions, for example, phosphate and cations, for example, Fe, Cu and Zn (Marschner et al.,1986; Gerke, 1993; Gerke et al., 1994; Rengel et al., 1998; Beißner and Römer 1998). Induced chemical changes in the rhizosphere could be due to presence of micro-organisms and/or their exudates, changes in the pH through H^+ release, which is related to change in cation/anion uptake ratio, and to root exudates, which are of both high molecular weight exudates such as mucilage and ectoenzymes and low molecular weight exudates such as organic acids, sugars, phynolics and amino acids (Marschner, 1995). However, little information is available on chemical K mobilisation.

It is now well known that plants take up considerable amounts of non-exchangeable K, which is the K fraction not extractable by NH_4Acetate (Schachtschabel, 1937; Kuchenbuch and Jungk, 1984). However, plant species benefit differently from non-exchangeable K, since different species vary greatly in root physiological characteristics (Mengel and Steffens, 1985). The mechanisms employed by the plants for non-exchangeable K release are not clearly defined. A decrease of soil solution concentration, to a critical value of 2-3 µM, initiates release of non-exchangeable K from interlayer positions of clay minerals (Claassen and Jungk, 1982; Springob and Richter, 1998). Although exuded H^+ are reported to cause the release of non-exchangeable K (Kuchenbuch, 1983), there is evidence that above pH 4, H^+ have a negligible effect on release of non-exchangeable K (Springob and Richter, 1998). Hinsinger et al. (1992) observed that the interlayer K of phlogopite, embedded in agar, was completely lost in the close vicinity of 4 days old ryegrass roots. The authors suggested that due to root depletion of rhizosphere K, the exchange equilibrium is shifted with the resulting release of interlayer K and expansion of the interlayer space of the mineral. Evidence also exists that addition of citric acid, in a quantity analysed in the rhizosphere of the proteoid roots of white lupine, increased the amount of non-exchangeable K extracted by electro-ultrafiltration (EUF) (Steffens and Zarhoul, 1997). Under K deficiency conditions, maize increased the amounts of low molecular weight exudes, and the amounts of sugars and organic acids were shifted in favour of the organic acids (Kraffczyk et al., 1984). The authors also reported that the proportion of malic acid increased with increasing K supply, while the dominating citric and oxalacetic acid decreased.

The objective of this study was to investigate whether root exudes, as measured in stressed white lupine plants (Gerke, 1993), influence the release of non-exchangeable potassium.

To carry out this objective a sandy clay loam soil, in which sugar beet had taken up much K from the non-exchangeable fraction, was desorbed for 72 hours, using different concentrations of malic and citric acid in 0.01 M $CaCl_2$ solution.

Materials and Methods

To study the effect of some organic acids, found in the root exudates of K deficient plants, on the K release from the sandy clay loam soil, the soil was desorbed with different concentrations (0-1000 µM) of citric acid and malic acid, in 0.01 M $CaCl_2$ solution, with the same Ca^{++} concentration as the soil solution. The acid concentrations were chosen in the range of citric acid concentrations found in the rhizosphere of phosphorous deficient white lupine, with a maximum of 1 mM in soil solution.

To study the changes in pH as a result of reactions occurring in the soil in relation to desorption by the organic acids, the pH of the acidic solutions were adjusted to 7.2 using NaOH. The desorption experiment was conducted in a cold laboratory at 6 °C, so as to minimise the degradation of organic acids by micro-organisms. Figure 1 shows the experimental set-up used for conducting the experiment. The soil was sieved through a 2 mm sieve and one gram air dry soil was placed on a filter paper placed in a glass funnel. The desorption was carried out for 72 hours. For each treatment, 30 mL of the relevant concentration of the organic acid solution were poured on the soil. At 12 hours intervals the clip was opened, the solution filtered in the glass beakers and the percolate was analysed for K. Then another 30 mL of the desorption solution were added to the soil. The K concentration in the percolate was determined by flame photometry. After that the pH values of the percolate were determined. Each treatment was replicated twice.

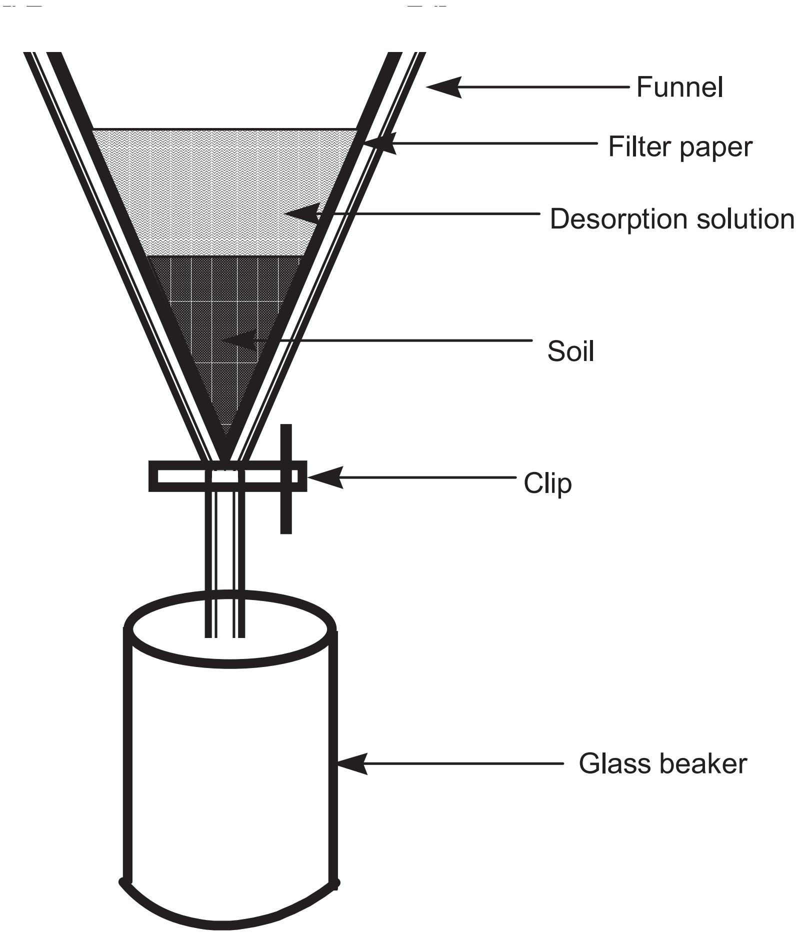

Fig. 1 *The experimental set-up used for desorbing a sandy clay loam soil with different concentrations of organic acids in 0.01 M* $CaCl_2$ *solution.*

Statistical Analysis

The data were statistically analysed using analysis of variance (ANOVA), where significant differences were found, mean separation was conducted using the Tukey test.

Results

The K concentrations in the solution, after desorption with the different concentrations of citric acid in 0.01 M $CaCl_2$, were significantly ($p \leq 0.05$) higher than K concentrations in the solution after desorption with $CaCl_2$ alone or the control (Fig. 2). For all desorption intervals, the K concentrations in the solutions of the different concentrations of citric acid did not differ significantly. However, significantly ($p \leq 0.05$) higher K concentrations were found in the solution after 12 hours as compared to the other time intervals, and between 24 and 72 hours.

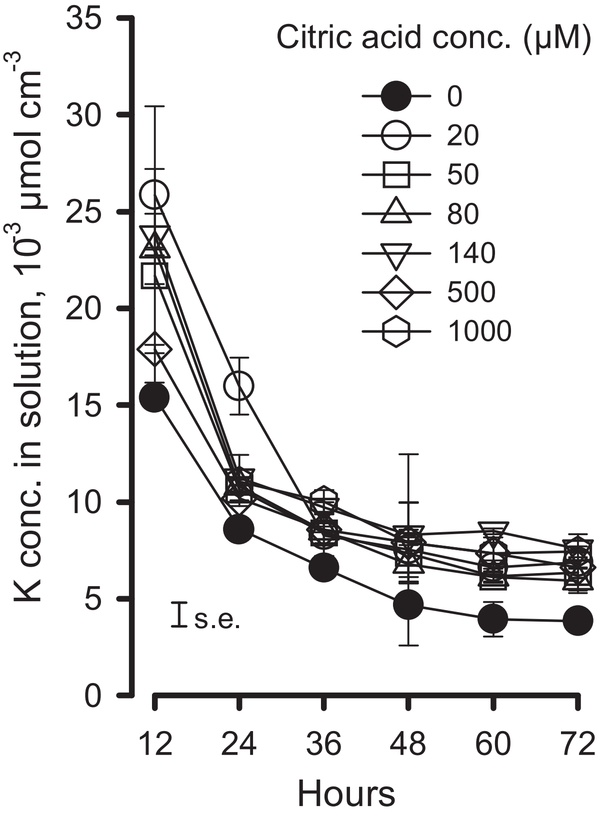

Fig. 2 *Potassium concentrations in the percolate after desorbing with different concentrations of citric acid in 0.01 M $CaCl_2$ solution at 12 hours intervals.*

Figure 3 shows the K concentrations in the solution, after desorbing with different concentrations of malic acid in 0.01 M $CaCl_2$, and only with 0.01 M $CaCL_2$ solution. In general and depending on the acid concentration, the K concentrations in the solution were either equal or higher than those found in the control. As compared to the control, significantly higher K concentrations ($p \leq 0.05$) in the solution were found, only after desorbing with 500 µM and 1000 µM concentrations, however, by the latter, at 48 till 72 hours.

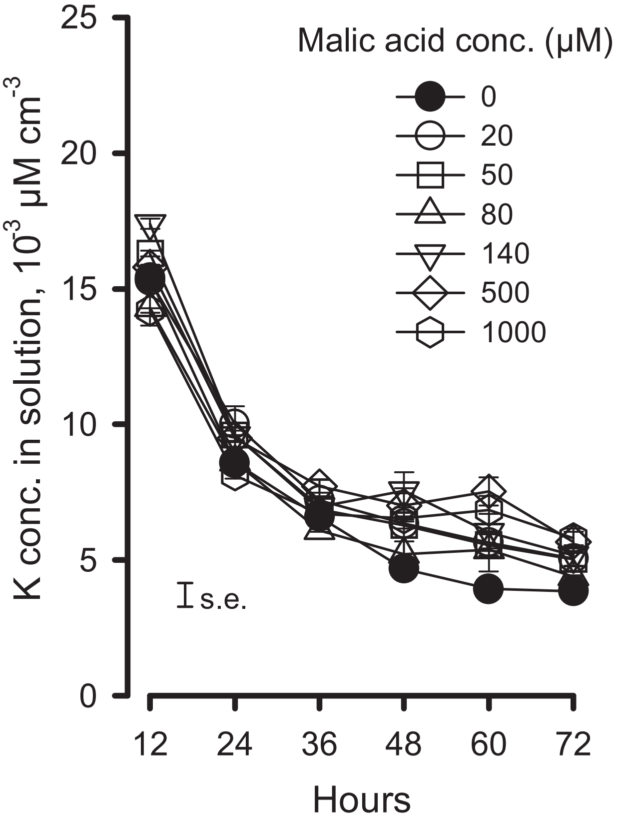

Fig. 3 *Potassium concentrations in the percolate after desorbing with different concentrations of malic acid in 0.01 M $CaCl_2$ solution at 12 hours intervals.*

Except for desorption with 80 µM, which for unknown reasons, had low K concentration in solution, no significant differences were found in the K concentrations in solution among the other different acid concentrations.

Generally desorption by the different concentrations of citric acid, resulted in significantly ($p \leq 0.05$) higher K amounts as compared to desorption by the different concentrations of malic acid and by the control at all the time intervals (Fig. 4 and 5). It is noteworthy that within citric acid except for the 140 µM concentration, the 20 µM acid concentration desorbed significantly ($p \leq 0.05$) higher K amounts as compared to the other acid concentrations (Fig. 4). At 500 and 1000 µM concentrations, malic acid desorbed significantly ($p \leq 0.05$) higher K amounts as compared to control only at the 60 hours interval. Within malic acid, except for the 80 µM concentration, all other acid concentrations did not differ significantly in the amount of desorbed K (Fig. 5).

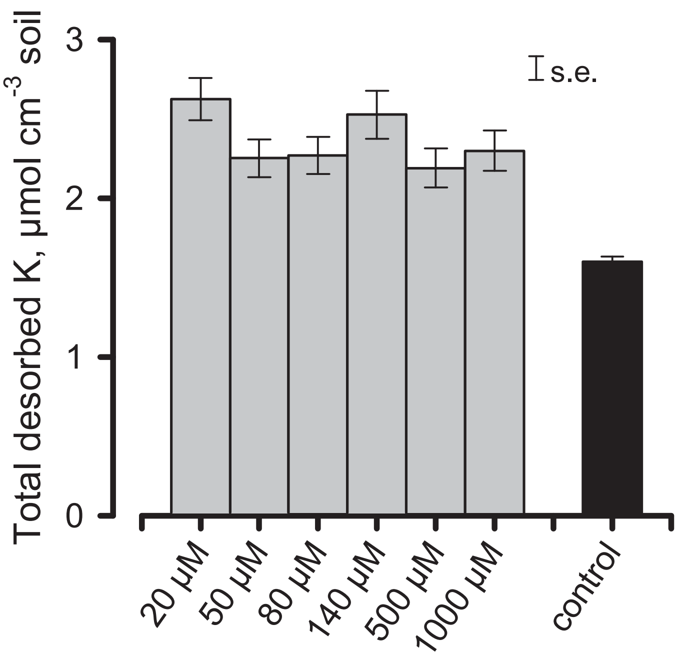

Fig. 4 *Cumulative desorbed K amounts in 72 hours after desorbing a sandy clay loam soil with different concentrations of citric acid in 0.01 M $CaCl_2$ solution.*

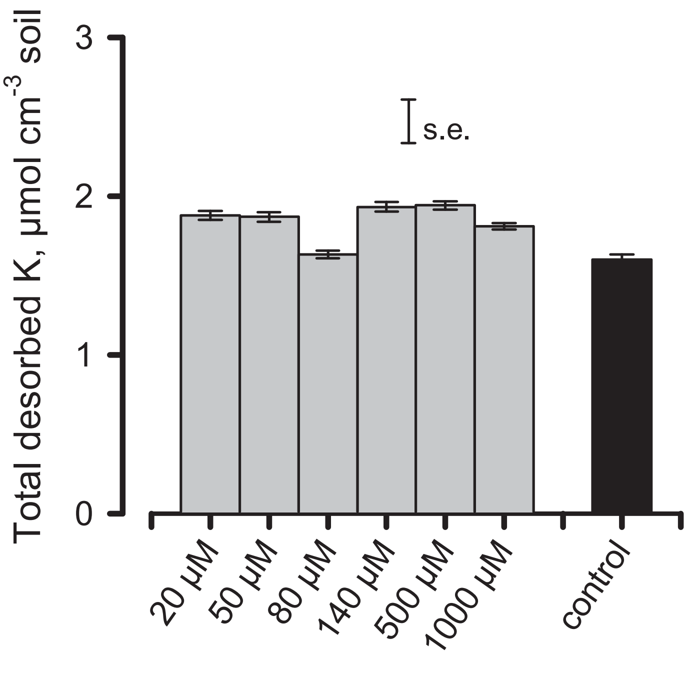

Fig. 5 *Cumulative desorbed K amounts in 72 hours after desorbing a sandy clay loam soil with different concentrations of malic acid in 0.01 M $CaCl_2$ solution.*

The pH effect

The pH values of the percolate, after desorption by the different concentrations of the organic acids at the different time intervals are presented in table 1. As can be seen, there was no difference in pH values between $CaCl_2$ alone and $CaCl_2$ plus organic acid. Since the soil had a very high buffering power, the pH values were not changed much from the initial value except for a slight decrease in pH found in the percolate after the first 12 hours of desorption. A general observation shows a trend to more acidification after desorption by malic acid.

Table 1 *The pH values of the percolate after desorbing a sandy clay loam with different concentrations of citric and malic acids in 0.01 M $CaCl_2$ solution (initial solution pH = 7.2)*

	Organic acids conc.					
Hours	0	20	50	80	500	1000
			pH			
Citric acid						
12	6.63	6.78	6.83	6.84	6.78	6.74
24	6.63	6.89	7.02	7.09	7.06	7.01
36	6.84	7.15	7.08	7.22	7.13	7.15
48	6.85	7.14	7.04	7.32	7.15	7.15
60	7.16	7.18	7.15	7.18	7.10	7.15
72	6.92	7.15	7.20	7.27	7.20	7.23
Malic acid						
12	6.63	6.60	6.66	6.78	7.23	6.81
24	6.63	6.65	6.22	6.90	6.93	6.97
36	6.84	6.87	6.91	7.10	7.50	7.54
48	6.85	6.80	6.86	6.89	6.95	7.00
60	7.16	6.82	6.90	7.05	7.55	7.62
72	6.92	6.83	6.98	7.55	7.68	7.69

Discussion

The results of the last chapter, showed strong evidence to the existence of some processes which were not considered by the model. Among such processes, chemical mobilisation of nutrients by the root exudates was contemplated as a possible reason why under low K conditions, the model was not able to predict actual uptake measured by the plants. As was mentioned in the introduction, K deficient plants exude particular organic acids in higher quantities in comparison to

K sufficient plants. Kraffczyk et al. (1984) reported that although the total quantity of exuded organic acids was not affected by K nutrition, nevertheless, malic acid increased with increasing K supply, whereas oxalacetic acid and citric acid dominated at low K supply. Based on these findings, this study was conducted to investigate the effect of some organic acids, found in the root exudates of K deficient plants (Kraffczyk et al., 1984), on the release of K from the clay minerals of the sandy clay loam soil used throughout this study.

Two interesting points were found: 1) all concentrations of citric acid used, desorbed significantly higher amounts of K as compared to the amounts desorbed by $CaCl_2$ solution without citric acid. 2) The maximum desorbed K amount was already achieved at 20 µM citric acid concentration. This means that citrate could enhance the release of K. Similar enhancement of K release by citric acid was reported by Steffens and Zarhoul (1997), Meyer and Jungk (1993) from loess soil and Song and Huang (1988) from different clay minerals. Malic acid, on the other hand, had no effect on K release, since it was not able to desorb higher K than a $CaCl_2$ solution alone. It is noteworthy that Song and Huang (1988) reported a 3 times faster rate of K release from biotite in oxalic acid solution, as compared to the release rate in citric acid solution. The difference in K release ability between these organic acids was attributed to differences in the amounts of organic ligands and H ions generated by organic acids, and to the complexing ability of the ligands. Meyer and Jungk (1993) found considerable differences in the effectiveness of the different organic acids in mobilising K. Their results contrasted with those of the former authors, where the latter authors showed a sequence of increased mobilising effect in the order of : citric acid > malic acid > oxalic acid > fumaric acid. It might have been that the mobilising effectiveness depended on the type of desorbed mineral.

The important question is the mechanism by which the organic acids release K from clay minerals. Phosphorous mobilisation by organic acid is based on ligand exchange (phosphate against organic acid molecules), whereas the higher solubility of metallic cations such as Fe, Al, Zn and Cu is based on building soluble complexes (Gardener et al.,1983; Gerke, 1994a). Nevertheless, these factors do not play a role in K mobilisation, thus other mechanisms must be responsible for K release from clay minerals. The suggestion of Song and Huang (1988) seems plausible. The authors propose that the OH^- and $COOH^-$ groups, of the low molecular weight organic acids, form metal organic complexes with the metal ions (Al, Fe, Mg) of the mineral structures such as clay minerals. This results in an accelerated decomposition of the minerals. Song and Huang (1988) explained that "The weakening of the metal -O bonds by the protonation of surface OH^- groups and the formation of inner sphere surface complexes with organic ligands (Stumm et al., 1985) certainly enhance the mineral dissolution."

In this experiment, the results showed no effect of the pH on K release from clay minerals. Our results contrast with other authors who reported greater effect of protons on K release. This effect occurs either by exchanging K bound between the clay mineral layers with protons, or by decomposing the minerals and setting the interlayer K free (Kuchenbuch, 1983; Meyer 1993).

It seems that the K release depends on the kind of organic acid. The fact that oxalate was especially effective for K release (Song and Huang, 1988) merits more attention, since, especially for sugar beet, the exudation of oxalate under stress, for example, P deficiency was more intensive than citrate (Beißner and Römer, 1995). Moreover, Kraffczyk et al. (1984) found that in the exudates of K deficient maize plants, oxalate and citric acids were dominant. From these results and discussion, it could be possible that wheat and sugar beet were probably capable, at low K supply, on a sandy clay soil, of increasing oxalate/ citrate exudation and as such were able to release more K as a consequence of an accelerated "biochemical weathering" of the K bearing clay minerals. The result could have been a higher K uptake, which is exhibited in the narrow space between the root surface and the soil solid phase. Obviously, this effect was not detected when measuring the K concentration in the soil solution, and this in turn led to an underestimation of the calculated K uptake.

However, it remains unclear why the maximum K release was established by concentrations as low as 20 µM, whereas higher citric acid concentrations were unable to desorb higher amounts of K. It is thinkable that this was due to complexing of Ca^{++} of the $CaCl_2$ solution by citric acid and this lowered the citrate concentration in the desorption solutions. Calcium citrate precipitation can occur at high calcium concentrations in the soil solution (Dinkelaker et al., 1989).

Moreover, it can not be ascertained whether the K release by organic acids was high enough to increase the K concentrations in the soil solution to the necessary level, by which the measured K uptake was possible, or whether there were other mechanisms, by which plants increase the K concentrations in the rhizosphere. The answers to these questions are beyond the scope of this study and further in depth investigations are needed in order to be able to answer these questions.

Conclusions

1. Citric acid enhanced K release from a sandy clay loam soil, whereas malic acid did not release more K than a $CaCl_2$ solution with the same Ca^{++} concentration as that found in the soil solution.
2. Already citric acid concentrations, as low as 20 µM, released significantly higher K amounts than the control. An increase up to 1000 µM, had no further effect on K release from soil.
3. Further research under natural conditions is necessary in this area, to quantify the K release by the organic acids, reported in the exudates of K deficient plants, especially the role of oxalacetic acid, which is reported to be more effective in K release from clay minerals, and which is dominant in the root exudates of K stressed sugar beet and maize plants.

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Chapter 7

Epilogue

Epilogue

This research yielded results, which showed that the various studied plant species had not only differing K efficiency, but also differing efficiency mechanisms.

Nutrient efficiency can be looked upon from different angles, depending on its definition. Considering nutrient efficiency with emphasis on productivity, it is of vital importance to differentiate between the basic criteria by which efficiency is regarded, whether absolute or relative yield. There is much controversy concerning the nutrient efficiency resulting from unclear separation between these yield forms. For example, Claassen (1989) concluded that sugar beet is less K efficient than wheat, since it obtained only 80 % yield, on the unfertilised relative to optimally K supplied plots, whereas wheat had 100 % relative yield. The results obtained in this study contrast with those findings. In the field experiment and based on terms of absolute yield sugar beet proved to be more efficient than wheat, since it was able to produce much more higher dry matter yield (200 dt ha^{-1}) as compared to wheat (60 dt ha^{-1}). On the other hand, considering the relative yield both plant species had similar K efficiency, both producing nearly 80 % relative yield on the unfertilised treatments.

The different plant species, which proved to be K efficient, had various mechanisms for attaining such efficiency. For example, wheat and sugar beet obtained the same relative yield employing completely different mechanisms or different components of an efficiency mechanism. Wheat had a high K utilisation efficiency, where it required low tissue K concentration to grow optimally, moreover, it had the advantage of a large root system, which allowed for more spatial K accessibility and, consequently, a higher K uptake. The large root system means also a smaller needed influx, which could be covered by a small transport ability of the soil. In addition wheat had a low shoot growth rate, which indicated a low nutrient demand on the roots. Sugar beet, on the other hand, with a low K utilisation efficiency or a high internal K concentration, which resulted in a very high nutrient demand on the roots, a small root system and a very fast growing shoot had, nevertheless, the same K efficiency as wheat. The efficiency mechanism of sugar beet was based on a very high physiological activity of the roots, reflected in high uptake rates per unit root and time. Under K deficient conditions at low K concentrations in soil solution, the efficiency of plant species, which are able to grow and yield optimally, can not be characterised by uptake and utilisation efficiencies *per se*. If the rate of nutrient replenishment at the root surface is much lower than the capacity of the root cells to take up nutrients, uptake will be governed by the nutrient supply rather than by the nutrient uptake capacity of the root cells (Rengel, 1993). Hence, increased uptake capacity of the root cells, due to an increased expression of high-affinity nutrient uptake systems under nutrient stress (e.g. a greater number of transporters, a greater nutrient affinity or a greater rate of turnover of transporters), would have a negligible contribution to higher uptake efficiency for nutrients supplied by diffusion such as P, K, Fe, Zn and Cu (Rengel, 1999). In order to take up large amounts of K from the soil, there should be sufficient K in the soil solution. This means the first step, under K deficiency conditions, is to increase the K concentration in the soil solution, before uptake of sufficient K amounts can occur. Without K fertilisation, the only possibility to increase the K concentration in soil solution is by releasing K bound in the interlayer of the clay minerals. Plant species with a capacity to facilitate uptake of large K amounts at sub-optimal K levels should, therefore, be considered as K efficient. Could this mean the plants species considered as K efficient because of a higher I_{max}, should they also be able to increase K availability in the rhizosphere? In this study the sandy clay loam soil used is rich in K, however, the K concentrations in soil solution and exchangeable K were very low due to the high fixing capacity of the soil. Sugar beet was able to take up considerably higher K amounts than wheat under these low K conditions, indicating a higher ability to increase the K concentrations in the soil solution, and as such could be regarded as possessing a higher K efficiency than wheat. An interesting question, which can not be answered within the context of this research, is whether wheat would be able to take up K amounts as high as those taken up by sugar beet, if it had only half its root system and much higher internal K requirements.

Nutrient efficient cultivars have great agronomic significance, since they represent an important adjunct to fertiliser use policies, where the soils are problematic and fertilisation efficiency is decreased by various climatic, physical and biochemical factors, as well as an important gene pool for plant breeders for breeding programs, aiming for incorporating nutrient efficiency mechanisms in, otherwise, economically important cultivars. Secondly, they offer a means for ecologically protecting agricultural strategies.

Several uncertainties, related to nutrient loss and dependence of nutrient availability on biophysical factors, face the characterisation of nutrient efficiency under field conditions (Sauerbeck and Helal, 1990). However, expressions of nutrient efficiency by species growing in the field are realistic, since, for example, root morphological development and physiological activity are affected by the physical and biochemical soil conditions and their interactions, that is have a direct effect on nutrients uptake efficiency. The plant species studied under controlled conditions, showed the same tendency to K efficiency and similar mechanisms as those grown under field conditions. Nevertheless, the K uptake and K influx of plant species grown in the growth chamber, were by far less than those of the plant species cultivated in the field. This indicates that under natural conditions, the plants exhibited higher K efficiency, especially so, that plant species under controlled conditions, showed visual K deficiency symptoms which were not detected in field grown plants. It could have been that some factors such as more K availability, little root competition among the roots, larger and different root architecture and K uptake from deeper soil layers contributed to the higher influx measured in the field. But as stated before K concentrations were low in the soil used in this research. Moreover, interlayer bound K must be released before any appreciable amounts could be taken up. It might have been that the influence of some climatic, physical or chemical soil conditions in the field, triggered some physiological or chemical responses in the plants which led to higher K release. A possible cause could have been the acidification of the rhizosphere by plant roots, through light dependent active excretion of H^+ (Mengel and Malissiovas, 1982). According to the same authors the passive release of organic anions, accompanying the H^+ excretion, might be of vital significance for many reactions occurring in the rhizosphere.

Evaluation of the use of a simulation model for calculating K uptake

The results of this study, combines both experimental and simulation work as described in the different chapters. Using the simulation model (NST) of Claassen (1994) proved to be essential for generating valuable information, pertaining to understanding the K dynamics in the rhizosphere, and to check our understanding of the concepts underlying K uptake by a growing root system. The simulation of K uptake allowed for an access to not easily measurable data such as K concentrations at the root surface, and the processes involved in K uptake as related to plant and soil factors, since nutrient availability in soil and plants ability to acquire nutrients are the basis for supplying plants with mineral nutrients (Jungk and Claassen, 1997). Quantifying the significance of the contribution of individual soil and plant parameters to K uptake, was possible through sensitivity analysis.

The agreement between calculated and measured K uptake, by various plant species reported in the literature, for example, (Silberbush and Barber, 1984; Claassen, 1994; Steingrobe and Claassen, 2000) and in some cases in this study, suggests that the main concepts underlying nutrient uptake are described and understood. However, the discrepancy observed between calculated and measured K uptake at some instances, for example, K uptake of sugar beet in the field without K fertilisation, unveiled that the model does not consider some vital processes in the rhizosphere such as chemical mobilisation, which might be responsible for improving K availability.

The central point revealed by K simulation is that the only possibility to cover the gap between calculated and measured K uptake is through higher K concentrations in the soil solution. The diffusive flux is a function of the concentration gradient (ΔC_L) between the soil solution (C_{Li}) and concentration at the root surface (C_{L0}). At low concentration gradients, K transport rates in the soil will be limiting K uptake. As such and as was shown in the sensitivity analysis, increasing the available K amounts alone, did not fully explain the under-prediction of the calculated K uptake, as was shown by the calculated uptake at various buffer power values. Hence, it was concluded that root exudates might have increased the soil solution K concentration, with the effect that sugar beet was able to take up considerably higher K than was possible under the prevailing conditions. This increase in C_{Li} was not considered by the model.

Prospects for future research

As was stated earlier, uptake of non-exchangeable K by plants has been known for long (Schachtschabel, 1937). However, the mechanisms employed by plants to release this K fraction are not clearly understood. Some authors (Claassen and Jungk, 1982; Hinsinger et al., 1992) explained this phenomena by extreme depletion of K in the rhizoshere by root uptake, decreasing the C_{L0} to critical concentrations (2-3 μM) which triggers K release from the interlayer of clay minerals. Others reported significant K release from clay minerals through the action of organic acids, namely citric and oxalacetic acids, from different soil types and clay minerals (Song and Huang, 1988; Meyer, 1993; Steffens and Zarhoul, 1997). Some authors proposed that K release from clay minerals is brought about by the effect of H^+, which exchange for K (Kuchenbuch, 1983; Meyer, 1993). Others attributed that to formation of metal organic complexes from the OH^- and $COOH^-$ groups of the low molecular weight organic acids and the metal ions (Al, Fe, Mg) of the mineral structures such as clay minerals, which result in an acceleration of the decomposition of the minerals and K release (Song and Huang, 1988).

The exact mechanisms with which plant roots cause the release of interlayer bound K, and increase the soil solution concentration in the rhizosphere through root exudates, merit closer in-depth investigations with the aim of understanding and explaining the principles of chemical mobilisation of K in the rhizosphere. The type of root exudates important for K release from the clay minerals, and the effect of the K nutrition on the composition of the root exudates are research areas where need of information is vital.

It would be of interest to investigate the role played by the radiation intensity in acidifying the rhizosphere by light dependent active excretion of H^+ by the plant roots (Mengel and Malissiovas, 1982), and to study the significance of the organic anions, passively released with the H^+, for several reactions which are taking place in the rhizosphere.

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