

Potassium Efficiency of Different Crops Grown on a Sandy Soil under Controlled Conditions

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Abstract: The objective of this work was to study K efficiency of different crops and determine the plant parameters affecting it. The study was carried out using 14 different crops and cultivars grown on a sandy soil rich in humus, with two potassium fertilisation levels under controlled conditions. The studied crops showed different K efficiency reflected in different dry matter yield production in unfertilised relative to fertilised treatments. All crops had, at low K supply, less than optimum K concentration in dry matter, indicating that the soil K concentration did not meet the K requirement of the plants. Thus, the ability to produce high dry matter yield indicated superior adaptability to K deficiency. The efficiency mechanisms employed by the different crops were low shoot growth rate and/or high root length - shoot weight ratio and a high uptake rate per unit root, i.e. the influx, or low internal K requirement. Crops with high influx had higher calculated concentration gradients, since they caused further decrease of the concentration at the root surface. As such, they were able to create steeper concentration gradients between bulk soil solution and root surface. This resulted in higher diffusive flux to the roots.

Key words: Nutrient efficiency; potassium; root density; influx

INTRODUCTION

It is now well known that plant species and even cultivars within a species differ in their nutrient efficiency (Cakmak *et al.* 1997; Fageria *et al.* 2001; El Dessougi *et al.* 2002; Bhadoria *et al.* 2004). Efficient species or cultivars are those able to grow and yield better under deficiency conditions as compared to inefficient species. Efficient species have either

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certain morphological or physiological characteristics that increase uptake or utilisation of nutrients, or they are able to chemically change the rhizosphere to improve the availability of nutrients (Sattelmacher *et al.* 1994).

Several workers found varying K efficiency among different plant species and genotypes. For example, El Dessougi *et al.* (2002) showed that wheat had a higher agronomic K efficiency than barley. Sadana and Claassen (1999) showed, in a pot experiment, that sugar beet is more K efficient than wheat and maize. Hence, varying K efficiency may be due to variations in internal requirements of the plant or use efficiency (Trehan and Claassen 1998; Zhang *et al.* 1999; Fageria *et al.* 2001). 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 Foehse *et al.* (1988). Other reasons for efficiency could be the K uptake ability of the plants, i.e. acquiring K from the soil or solution and accumulating it in the shoots. This depends on the density of roots and on the efficiency of the single roots to take up K or the influx (El Dessougi *et al.* 2002; Bhaduria *et al.* 2004).

One of the possible strategies of sustainable land use, which enables maximum output with minimum input, sustains resources and conserves 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 nutrients such as K could have a significant agronomic importance.

The objective of this work was, therefore, to study K efficiency of different crops and to determine the plant parameters affecting this efficiency.

MATERIALS AND METHODS

The 14 crops and cultivars used in this study and the number of plants per pot and number of days between sowing and harvest are shown in Table 1. The plants were grown in a growth chamber with a day/night regime of 16/8 hours, temperature of 25°C/15°C for cotton and maize and 20°C/15°C for all other crops and relative humidity of 70%. The photosynthetic active radiation during the day time was 250 $\mu\text{E m}^{-2} \text{s}^{-1}$.

Potassium efficiency of crops

Plastic pots of 1.2 liter capacity were filled with 1.2 kg sandy soil rich in humus from Hodenhagen North Germany, having pH 5.2, 3 % clay, 7 % silt, 5.5 % humus and $537 \mu\text{mol kg}^{-1}$ soil exchangeable K. Control (no K added) and 300 mg were used of KCl. Other nutrients were added per pot as follows: 200 mg N as NH_4NO_3 , 50 mg Mg as $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, and 200 mg P as Ca (H_2PO_4)₂. The plants were watered daily to 20% moisture content by weight. Three pots per treatment were left un-planted as control. Each treatment was replicated 3 times. The experiment was carried out in a completely randomized design.

At harvest, the plants were cut at the soil surface and 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 and sub-samples 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 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). The roots of the sub-sample were cut in approximately 0.5 cm pieces and distributed evenly over a 0.2 mm sieve with 314 cm^2 surface area. The sieve was placed under a microscope and 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 was calculated using the following equation:

$$RL = \frac{\pi \cdot NF}{2 \cdot nH} \quad (1)$$

where

N = Sum of the intersections of all measurements, F = Sieve surface area (cm^2), N = Count number and H = Hairline length (cm).

Table 1. Number of days between sowing and harvest and number of plants per pot at first (t_1) and second (t_2) harvest in 14 crops and cultivars

Crop	Time to harvest (days)		Number of plants pot^{-1}	
	t_1	t_2	1 st harvest	2 nd harvest
Spring wheat (<i>Triticum aestivum</i> L.) cv. Star	15	32	4	4
Winter wheat (<i>Triticum aestivum</i> L.) cv. LPI 601	15	32	4	4
Spring barley (<i>Hordeum vulgare</i> L.) cv. Marina	15	32	4	4
Winter barley (<i>Hordeum vulgare</i> L.) cv. Trasco	15	34	4	4
Rye grass (<i>Lolium perennial</i> L.) cv. Locarno	14	34	4	4
Oilseed rape (<i>Brassica napus</i> L.) cv. Liraget	16	34	2	2
Sugar beet (<i>Beta vulgaris</i> L.) cv. Aries	16	34	3	3
Sunflower (<i>Helianthus annuus</i> L.)	17	34	3	3
Maize (<i>Zea mays</i> L.) cv. Konsul	14	34	4	4
Maize (<i>Zea mays</i> L.) cv. Ferris	14	34	4	4
Spinach (<i>Spinacea oleracea</i> L.) cv. Subito RZ	17	34	3	3
Faba beans, (<i>Vicia faba</i> L.), cv. Victor	17	32	4	3
Elephant grass (<i>Pennisetum purpureum</i> L.)	16	34	4	3
Cotton, (<i>Gossypium barbadense</i> L.)	15	32	4	4

Potassium efficiency of crops

The sub-sample length and weight 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} :

$$r_0 = \sqrt{\frac{RFW}{\pi RL}} \quad (2)$$

where

RFW = Root fresh weight (g), and 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):

$$RL_v = \frac{RL}{SV} \left(\text{cm} \text{cm}^{-3} \right) \quad (3)$$

Average half distance between neighbouring roots (r₁): 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:

$$r_1 = \sqrt{\frac{1}{\pi RL_v}} \quad (4)$$

Extension of the depletion zone (Δx): The extension of the K depletion zone (Δx) is the distance to which K can be depleted around the roots. It was calculated from the effective diffusion coefficient (D_e) and the time difference between the two harvests (t) as follows (Syring and Claassen 1995) :

$$\Delta x = \sqrt{\pi D_e t} \quad (5)$$

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

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

where

SW = Shoot dry weight (g), t = Time (days) and 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) as follows:

$$\ln = \frac{u_2 - u_1 \ln \left(\frac{RL_2}{RL_1} \right)}{t_2 - t_1 RL_2 - RL_1} \quad (7)$$

where

U = Nutrient element content in the plant (mol), RL = Root length (cm) and 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):

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

where

D_L = K diffusion coefficient in water ($\text{cm}^2 \text{ s}^{-1} = 1.98 \times 10^{-5}$), Θ = Volumetric water content ($\text{cm}^3 \text{ cm}^{-3}$), f = Impedance factor after Kaselowsky (1990), r_0 = Root radius (cm), and RL_v = Root length density (cm cm^{-3}).

Soil solution

The soil solution was obtained by the 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 soil, displacing the soil solution downwards where it is taken in glass beakers. To exclude soil solution dilution by the added water, 4% potassium thiocyanate was added as a marker to the water, and the soil solution obtained was then tested with 5% FeCl_3 . A red colour 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 gramme of field moist soil was 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 was measured in 0.01 M CaCl_2 in a 1.0:2.5 soil: solution ratio. Soil samples were dried at 105°C to constant weight, and the gravimetric water content was determined.

Statistical Analysis

The data were subjected to analysis of variance and the means were separated by the Tukey test.

RESULTS

Relative and absolute dry matter yield

Potassium efficiency of the different crops, expressed as the shoot dry matter yield of the unfertilised and the fertilised treatments, was highest for spring wheat (51%) and least for spinach (15%) (Table 2). Relative yield differed significantly ($P \leq 0.001$) among the different crops. Mean dry weight (mg plant^{-1}) ranged between 72 and 1000 under low K, and 183-4003 under adequate K supply (Table 2). Some of the crops; namely, barley, maize cultivars, sunflower, oilseed rape and spinach showed visual K deficiency symptoms in unfertilised treatments, especially spinach which was severely affected.

Potassium concentration in dry matter

The K concentration percentage in dry matter ranged between 0.31 and 1.09 for the unfertilised and 1.76 and 8.10 for the fertilised treatments (Table 2). The maize cultivars had the least K dry matter concentration in both treatments, whereas elephant grass, spinach and sugar beet had the highest K concentration in the unfertilised and fertilised treatments.

Root length-shoot weight ratio (RSR) and root length density

For the RSR (Table 3), no significant differences were found between fertilised and unfertilised treatments for all crops; however, the latter interacted significantly ($P < 0.05$) with fertilisation. Hence, wheat cultivars, spring barley, oilseed rape, faba bean and cotton had higher RSR in unfertilised than in 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 crops. As compared to fertilised treatments, it was 3-4 folds for maize, winter barley and sunflower, and 1-2 folds for elephant grass, spinach and sugar beet. Root length density (Table 4) differed significantly ($P \leq 0.001$) between crops. It was highest for faba bean and maize cv. Ferris and least for spinach and elephant grass.

Potassium efficiency of crops

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

Crop	Dry matter yield (mg plant ⁻¹)		Relative yield	K conc. in dry matter (%)	
	-K	+K		- K	+K
Spring wheat	264(0.04)	521(0.82)	51(2.2)	0.75 (0.02)	5.08 (0.03)
Winter wheat	286(0.03)	751(0.09)	38(2.4)	0.66 (0.03)	4.99 (0.05)
Spring barley	331(0.07)	974(0.12)	34(3.0)	0.48 (0.01)	4.79 (0.15)
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 cv. Konsul	1000(0.13)	4003(0.22)	25(1.2)	.31 (0.01)	1.76 (0.12)
Maize cv. Ferris	963(0.06)	620(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)
HSD (0.05)			12.6		

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

HSD = Highest significant difference, calculated after Tukey test
Values between brackets represent the standard errors of means.

Table 3. Relative shoot growth rate (RGRs) and root shoot ratio (RSR) of 14 crops grown on a sandy soil without (-K) and with (+K) K fertilisation

Crop	Relative shoot growth rate (d ⁻¹)		Root length-shoot weight ratio (cm mg ⁻¹)	
	-K	+K	-K	+K
Spring wheat	0.06 (0.01)	0.09 (0.03)	4.2 (1.03)	2.2 (0.32)
Winter wheat	0.07 (0.01)	0.12 (0.01)	4.3 (0.34)	5.3 (0.57)
Spring barley	0.08 (0.01)	0.13 (0.01)	5.8 (0.32)	3.1 (0.68)
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 cv. Konsul	0.15 (0.07)	0.21 (0.01)	(0.12)	4.9 (0.52)
Maize cv. Ferris	0.16 (0.01)	0.22 (0.01)	.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)
HSD (0.05)	0.09	0.12	5.2	6.7

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

HSD = Highest significant difference, calculated after Tukey test

Values between brackets represent the standard errors of means.

Potassium efficiency of crops

Table 4. Root length density (RL_v) and the average half distance between the roots (r_l) of 14 crops grown on a sandy soil without K fertilisation

Crop	Root length density cm cm ⁻³	Average half distance cm
Spring wheat	4.4 (0.896)	0.30.(028)
Winter wheat	5.0 (0.545)	0.3 (0.014)
Spring barley	7.7 (0.857)	0.2 (0.011)
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 cv. Konsul	7.1 (0.735)	0.2 (0.011)
Maize cv. 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)
HSD (0.05)	7.1	0.2

HSD = Highest significant difference, calculated after Tukey test
Values between brackets represent the standard errors of means.

Average half distance between neighbouring roots (r_1) and extension of the depletion zone (Δx)

Average half distance between neighbouring roots (r_1) ranged between 0.2 and 1.1 cm for the different crops. The cereals had more or less similar r_1 , whereas r_1 was intermediate for sugar beet, oilseed rape and sunflower and largest for spinach. The value of the extension of the depletion zone (Δx) was 0.24 cm for the crops studied. This value was equal or smaller than r_1 value of all crops indicating that no inter-root competition for K took place.

Relative shoot growth rate (RGR_s)

Except for the maize cultivars, all cereals as well as faba bean had low RGR_s (Table 3), whereas oilseed rape and sugar beet had nearly double RGR_s with and without fertilisation. Spinach and elephant grass had even 3 and 2 times higher RGR_s in fertilised than in unfertilised treatments. For the RGR_s, highly significant ($P \leq 0.001$) differences were found between the fertilisation levels and between crops, but their interaction was not significant.

Total K uptake and influx

Potassium uptake varied significantly ($P \leq 0.001$) between the fertilisation levels (Table 5). Generally, all crops had a low K content in the unfertilised treatments. Wheat cultivars, rye and cotton had more or less similar K content in their dry matter without fertilisation. However, K content did not follow the same pattern in fertilised treatments. Elephant grass had the least uptake rate in both treatments (Table 5).

The influx varied greatly among the crops both with and without fertilisation. Sunflower had the highest K influx in the unfertilised treatments followed by elephant grass and oilseed rape, and winter barley had the least influx. In the fertilised treatments, oilseed rape had the highest influx followed by sugar beet, spinach and elephant grass. The least influx was found for maize cv. Konsul. Highly significant ($P \leq 0.001$) differences were found between the two fertilisation levels.

Potassium efficiency of crops

Concentration difference in soil solution (ΔC_L)

The concentration difference, (ΔC_L) depends mainly on the K influx and differed, therefore, greatly between the crops (Table 6). The calculated values of ΔC_L for some crops, such as winter wheat, barley and faba bean,

were smaller than the initial soil solution concentration (C_{Li}) and as such could explain the diffusive flux to the roots. However, the calculated ΔC_L values for some crops, such as sunflower, sugar beet and elephant grass, were by far greater than the C_{Li} of the bulk soil.

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

Potassium concentration of soil solution after the harvest of plants varied depending on the crop species (Table 7). Wheat and maize cultivars decreased the K concentration in the soil solution to around one third of the initial concentration of the un-planted control ($15 \mu\text{mol L}^{-1}$). For some crops, such as sugar beet, spinach and elephant grass, the K concentration in the soil solution was up to 6 times the concentration found in un-planted soil ($15 \mu\text{mol L}^{-1}$).

Significant ($P \leq 0.001$) differences between the crops 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 ($20 \mu\text{mol 100}^{-1} \text{ g soil}$); crops such as elephant grass, spinach and sunflower decreased it by only around 10%.

Table 5. Potassium content and influx of 14 crops grown on a sandy soil without (-K) and with (+K) K fertilisation

Crop	Plant K content ($\mu\text{mol K pot}^{-1}$)		K influx ($10^{-14}\text{mol cm}^{-2}\text{s}^{-1}$)	
	-K	+K ^o	-K	+K
Spring wheat	201 (3.19)	2703 (53.8)	3.35 (1.04)	59.8 (19.2)
Winter wheat	194 (7.99)	3832 (78.9)	1.48 (0.12)	34.4 (3.73)
Spring barley	164 (5.23)	4780 (57.2)	1.01 (0.10)	56.2 (11.9)
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 cv Konsul	316 (3.59)	7183 (91.3)	.02 (0.33)	14.6 (0.65)
Maize cv. 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)
HSD (0.05)	74	2668	5.05	114

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

HSD = Highest significant difference, calculated after Tukey test

Values between brackets represent the standard errors of means.

Potassium efficiency of crops

Table 6. Initial K soil solution concentration of the bulk soil (C_{Li}), root radius (r_o), concentration difference in soil solution (ΔC_L) and calculated concentration at the root surface (C_{LO}) of 14 crops grown on a sandy soil without K fertilisation

Crop	r_o	ΔC_L	C_{LO}
Spring wheat	1.22 (0.021)	15.24 (0.48)	-0.15 (0.45)
Winter wheat	1.14 (0.005)	6.75 (0.61)	8.34 (0.11)
Spring barley	0.96 (0.031)	4.50 (0.44)	10.59 (0.52)
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 cv. Konsul	1.34 (0.117)	11.98 (0.48)	3.11 (0.49)
Maize cv. 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 crops, $C_{Li} = 15 \mu\text{mol L}^{-1}$

For calculating ΔC_L (Eq. 8), the following parameters were used: $D_L = 1.98 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ (\mathbb{C}) = $0.25 \text{ cm}^3 \text{ cm}^{-3}$, (f) = $1.58\mathbb{C} - 0.17$, Influx (see Table 5) and RL_v (see Eq. 8 and Table 4).

Values between brackets represent the standard errors of means.

Table 7. Exchangeable K and soil solution K concentration after growing 14 crops and cultivars on a sandy soil without K fertilisation

Crop	Exchangeable K ($\mu\text{mol 100}^{-1} \text{ g soil}$)	Soil solution K conc. ($\mu\text{mol L}^{-1}$)
Spring wheat	33.0 (0.64)	4.1 (0.27)
Winter wheat	25.3 (0.99)	2.6 (0.26)
Spring barley	26.6 (0.62)	16.2 (0.13)
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 cv. Konsul	28.8 (0.91)	14.7 (0.41)
Maize cv. Ferris	27.9 (0.52)	4.9 (0.52)
Faba bean	37.7 (0.68)	89.8 (0.55)
Elephant grass	48.4 (0.43)	87.7 (0.41)
Cotton	29.7 (0.40)	10.2 (0.29)
Control (unplanted)	53.7 (0.67)	15 (0.08)
HSD (0.05)	20.1	76.7

$C_{Li} = 15 \mu\text{mol L}^{-1}$ for all plant species.

HSD = Highest significant difference, calculated after Tukey test

Values between brackets represent the standard errors of means.

DISCUSSION

Plants growing in pots under controlled conditions are not able to express their nutrient 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 soil volume and the root system explores the whole pot with the result that the whole soil volume may supply nutrients to the plant.

The amount of K taken up by a plant depends on the root size and its distribution in the soil profile. Amount of K absorbed by each root segment partly depends on the soil volume it can exploit, that is the distance to the neighbouring roots. 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 of possible inter-root competition. Higher RL_v results in smaller average half distance between neighbouring roots (r_1). Smaller r_1 than the extension of the ion depletion zone (Δx) leads 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. The value of Δx was either equal or smaller than r_1 values of all crops. Hence, root competition probably was not the factor limiting K uptake.

The K efficiency, expressed as the dry matter yield without fertilisation compared with maximum dry matter yield, differed greatly among the different crops. Potassium efficiency could be due to differences in internal requirement and/or uptake efficiency (Sadana and Claassen 1999; El Dessougi *et al.* 2002). Potassium concentration in the dry matter is a measure of the nutritional status of the plant. Crops differ in their internal K requirements, which is the K concentration needed for producing about

90% of maximum yield (Foehse *et al.* 1988). For example, the optimum K concentration in dry matter for spring wheat lies between 3.3% and 4.5% and for sugar beet and spinach between 3.5% and 6% and 3.5% and 5.3%, respectively, (Bergmann 1993).

In this study for all tested crops, K concentration in dry matter on the unfertilised treatments was far below optimum internal concentration. At deficient K levels, the respective crops were able to accumulate only 16%, 12% and 10% of their optimum K requirement meaning that the crops were not able to accumulate enough K in the shoots. This indicates that for all crops K uptake was limited by K supply by the soil. However, crops with more yield, in unfertilised treatments, displayed a superior capacity to adapt to the existing soil conditions. Therefore, crops such as wheat could be said to have high utilisation efficiency, since it was able to produce more yield with an internal K concentration which was much lower than the optimum level. Spinach was incapable of high dry matter production and as such could be considered as having low use efficiency. This may have been because the very low K concentration in the soil solution of the nonfertilised treatments ($15 \mu\text{mol K L}^{-1}$), 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 the maximum yield (Foehse *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_s) and uptake efficiency of each root segment or influx. 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 RGR_s plants with a high shoot growth rate have a higher nutrient demand on the roots and vice versa (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.

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Lower RGR_s could be the reason behind the efficiency of some crops, for example wheat and rye. However, lower RGR_s is not necessarily associated with high efficiency, since crops like spinach and winter barley were not inefficient because of a high shoot demand for K on the roots. Sadana and Claassen (1999) found that sugar beet with the highest relative shoot growth rate is more efficient than either wheat or maize. They concluded that sugar beet efficiency is not because of low shoot demand on the roots, but because of a 4 times higher influx of the former as compared with the latter crops. Hence, shoot growth rate alone can not explain the differences in K efficiency of the different crops.

As explained above, nutrient acquisition is either due to more roots per unit shoot, which enable the plants to take up more nutrients, or high 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 (Cakmak *et al.* 1997; El Dessougi *et al.* 2002; Bhadoria *et al.* 2004). In this study, some crops, for example wheat and spring barley, possessed high uptake efficiency due to a high root length-shoot weight ratio and low RGR_s . Uptake efficiency of other crops, for example elephant grass, was mainly because of a low shoot demand on the roots and a very high influx.

Although all crops under study grew with the same initial K concentration of soil solution, some of them, such as sunflower, were able to have a high influx, whereas others had only one third of the formers' influx. This indicates that K influx depends on plant characteristics as well as soil conditions.

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 high K influx of sugar beet, as compared with wheat and maize, to the fact that sugar beet is able to decrease the C_{L0} to a much lower value than did the cereals. The theoretical C_{L0} values for some crops were such that

a diffusive flux to the roots, in the same order as the measured influx, was possible. In such cases, the efficiency mechanism could be a relatively larger root surface area than K requirement and, consequently, a smaller influx. In some crops, such as sunflower, elephant grass, sugar beet and oilseed rape, the concentration difference needed to drive 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 crops had developed mechanisms to release more K from the soil solid phase, e.g. by solubilisation through root exudates. This means that some processes, which were not included in the calculation of ΔC_{L1} , took place in the rhizosphere. These findings support those reported by Claassen (1994).

All crops were able to decrease the initial exchangeable K to different levels. On the other hand, K concentration of the soil solution except for some crops, e.g. wheat and maize cv. Ferris, remained relatively unchanged or even increased. The K concentration of the soil solution of sugar beet, spinach and elephant grass was 6 times higher than the initial soil K concentration. Similar results were found by N. Claassen (personal comm.) and Dieffenbach (1999).

It does not seem possible that, at such high soil K concentrations, these crops 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 . Moreover, after an adjustment phase, wheat and maize were able to grow with maximum growth rates at only 1 μM K concentration. Also, comparison between the C_{Li} and the theoretical ΔC_L showed that some crops 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 it 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

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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 that 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, e.g. in oilseed rape and spinach, or extremely low uptake rate per unit root, as in winter barley. These findings are in agreement with those of Foehse *et al.* (1988) who found that the studied crop species developed differing strategies for high P uptake efficiency. Some crops had large root systems others had high uptake rate per unit of root length. None of the crops showed a combination of high values of both uptake components.

CONCLUSIONS

1. Causes for high K efficiency are low shoot growth rate and/or high root length-shoot weight ratio or a high uptake rate per unit root or influx.
2. Differences in influx among crops 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.
3. Some crops even with high soil solution concentration are not able to have 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.
4. Further studies are needed to understand the exact mechanisms of K uptake efficiency of plants and the role of root exudates in solubilization of K in the rhizosphere.

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الكفاءة البوتاسيّة لأنواع مختلفة من المحاصيل أستثبتت في تربة رملية تحت ظروف متحكم بها

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المستخلص: هدفت هذه الدراسة الى تحديد الكفاءة البوتاسيّة والصفات النباتية المؤثرة فيها لعدد من أنواع المحاصيل. أجريت الدراسة باستخدام أربعة عشر مصوّلاً وصنفاً زرعت في تربة رملية غنية بالدبال، مع مستويين من السماد البوتاسي تحت ظروف متحكم بها. أظهرت المحاصيل قيد الدراسة اختلافاً في الكفاءة البوتاسيّة والتى انعكست في الفارق في إنتاج المادة الجافة في المعاملة غير المسمدة عند مقارنتها بالمعاملة المسمدة. عند الامداد البوتاسي المنخفض كل المحاصيل أنتجت مادة جافة أقل منها عند معدل الامداد البوتاسي المثالي، مما يدل على أن تركيز البوتاسيوم بالتربيه لم يف بحاجة النبات للبوتاسيوم. لذا فإن القدرة على إنتاج كمية كبيرة من المادة الجافة تدل على تكيف عال لنقص البوتاسيوم. تمثلت آلية الكفاءة في المحاصيل المختلفة في معدل نمو المجموع الخضري البطئ و/أو نسبة طول الجذور لوزن المجموع الخضري ومعدل الإمتصاص العالى لوحدة الجذر مما يعني التدفق أو الحاجة الداخلية المنخفضة للبوتاسيوم. كان لدى المحاصيل ذات معدل التدفق العالى ميل تركيز أعلى، لأنها تسببت في إنخفاض التركيز عند سطح الجذور، مما أدى إلى انحدار في ميل التركيز بين محلول التربة وسطح الجذور والذي نتج عنه دفق انتشاري عال نحو الجذور.

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