Crop Growth and Potassium Uptake as related to Plant and Soil Properties

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Introduction

Potassium concentration in plants is among the highest and therefore the amount needed for optimum growth is relatively high (see **Fig. 1**). The earth crust on average and similarly soils contain large amounts of K bearing minerals that often satisfy the plant demand but in some cases the K in those minerals is of low availability to plants leading then to K deficiency in crops. But crops may differ in their ability to grow under conditions of low K availability as is shown in **Fig. 1**.

Fig. 1: *Relative yield, dry matter yield and K uptake of potato, wheat and sugar beet grown on a sandy clay loam soil. The soil was K ''fixing'' and the unfertilized soil contained 782 pmol kg*$^{-1}$ *exchangeable K and a soil solution concentration of 4.2 µM. The fertilized soil (10 years 1000 kg K ha*$^{-1}$ *yr*$^{-1}$*) had 1074 µmol K kg*$^{-1}$ *exchangeable K and a soil solution concentration of 7.5 pM.*

Figure 1 shows yield and K uptake of potato, wheat and sugar beet grown in the field of a K fixing soil with a high total but low available K supply. The plants were grown with no K fertilization and with a sufficient amount of K fertilizer. Taking the yield of the unfertilized relative to the fertilized plot as a measure of K efficiency, i.e. capacity to grow under low soil K supply, it can be seen that potato was the less K efficient, yielding only 22% as compared to wheat and sugar beet that were similarly yielding around 80%. Looking at the absolute yields of harvested produce as well as the K uptake (total in shoots (leaves, beets, tubers and grain) at time of maximum shoot content) a further differentiation can be observed, i.e. sugar beet had a much higher dry matter production and higher K uptake at limiting K supply than wheat or potato. This shows that even though wheat and sugar beet were equally K efficient, the uptake efficiency or K acquisition of sugar beet was much higher.

Other research points in a similar direction. Sugiyama and Ae (2001) evaluated a long term fertilizer experiment on brown Andosol and found that potato was the less K efficient, yielding on the unfertilized soil only 19% of the fertilized plot. Sugar beet yielded 56% and winter wheat 101% on the unfertilized as compared to the fertilized plot. But sugar beet had the highest K uptake efficiency, i.e. it took up 114 K ha^{-1} while wheat absorbed 55 and potato 18 kg ha^{-1} for sugar beet, wheat, and potato, respectively. Alt and Ladebusch (1984) showed for horticultural crops that after 20 years of no K fertilization of a loamy sand, beans yielded almost 100% while spinach yielded only 30% not only among varieties of the same species of maximum yield. There are differences in K efficiency as was shown by Trehan (2000) for potato. The results show that there are differences in K efficiencies among crops partly because their requirement (K uptake at sufficient in K supply, see **Fig. 1**) differs but also because the capacity to absorb K at limiting K supply differs.

Differences in total K requirement are based on the size of the plants and on the internal requirement or use efficiency, as can be partly deduced from data of **Fig. 1**. But in the following we will concentrate on the reasons for differences in K uptake efficiency among plants. For this we will schematically describe the plant-soil system and the interaction between roots and soil and then analyse the plant factors that may be responsible for differences in K uptake from soil.

The soil-root system

Figure 2 shows the soil-root system for K in a simplified way. The root takes up K from the soil solution only, i.e. there is no direct transfer of solid bound K (exchangeable and interlayer K) to the root surface or to the site of uptake into the root which is the interlayer K) to the root surface or to the site of uptake into the root which is the plasmalemma or cell membrane. As the root absorbs K, its concentration at the root surface decreases and the resulting concentration gradient causes K transport to the root by diffusion.

Fig. 2: *The soil-plant root system with the main K pools in soil and their size*

Potassium transport to roots by mass flow is usually low because of the relatively low concentration in soil solution. The decrease of K in soil solution due to K uptake by plants causes the release of K from the solid phase, first by desorption from the exchangeable fraction and later from the interlayer of non-exchangeable K.

Potassium in soil solution of fertile agricultural soils varies between 100 and 500 µM (Claassen, 1990) and, mainly in sandy soils, it may reach values even above 1000 µM. In K fixing soils very low K concentration in solution may occur, like 5 µM, as we will see later. The amount contained in the soil liquid phase varies between 5 and 50 kg K h^{-1} which is much below plant requirement and therefore the desorption of K from the solid phase is a necessary process to cover the plant needs.

The amount of exchangeable but mainly of interlayer K depends on the clay content and on the clay mineral of the soil. Highly weathered soils that contain kaolinite have smaller amounts of exchangeable K and no interlayer K. But many soils contain 2:1 clay minerals which have a higher exchange capacity and with certain specify to bind K. Therefore, soils with 2:1 type clays contain more exchangeable K. If the layer charge of the crystal lattice is high, K between the layers is held so strongly that it hardly can be removed. The amount between the layers of the clay minerals may be very large (**Fig. 2**) and in many soils represents the main storage pool.

Plants take up K from the soil solution and since the exchangeable K is readily desorbed, most of it is easily available to plants. In soils with kaolinite, probably most of the exchangeable K will be used by plants but in soils which contain 2:1 clay minerals with specific binding of K, not all of the exchangeable K is exhausted by plants because non exchangeable K starts to be released (Kuchenbuch and Jungk, 1984; Bucher and Bihler, 1981). How much K a plant can use of the large pool of interlayer K depends on two

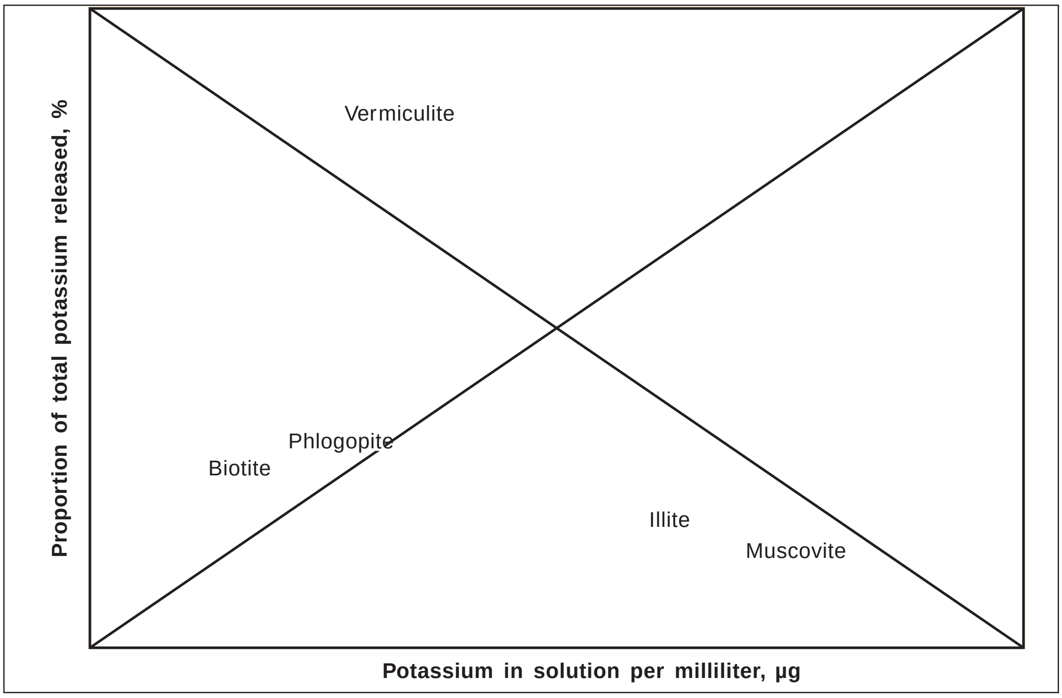

Fig. 3: *Release of K from different micaceous minerals suspended in I M NaCI solution versus concentration of K in solution at equilibrium (Black, 1968).*

Potassium in solution per milliliter, µg

major factors, i.e. the type of clay mineral and K concentration in the soil solution. This is illustrated in **Fig. 3** and **Table 1**.

Table 1: Proportion of total K released from different micaceous minerals at several micaceous external K concentrations in solution (taken from Fig. 3).

Mineral	K in sodium, µM			
	1000	100	25	5
Vermiculite	55	<80	100	100
Phlogopite	2	<80	100	100
Biotite	-	<80	100	100
Illite	-	5	15	35
Muscovite	-	-	1	6

It can be seen that as the K concentration in the bathing solution decreases the proporation of K released increases. At a K concentration of 100 µM, vermiculite, phlogopite and biotite release almost all of K and even illite already releases, 5%. This apparently low percentage has to be related to the total amount (see **Fig. 2**). i.e. if we assume interlayer K in solution, even muscovite would release appreciable amounts. Therefore, how much interlayer K a plant can reduce the K concentration to a low value and still have a high K influx (uptake per unit root and unit time i.e. mol cm^{-1} s^{-1}) and will be able to use a large proportion of the interlayer K.

The availability of a nutrient not only depends on amounts or concentrations in soil but also on its mobility in soil. The mobility is needed for nutrients to reach the root surface. Very mobile nutrients, like NO_3^- which is not absorbed to the soil particles, can move several cm within the active life time (one to three weeks) of a root. For these ions the whole soil volume will be depleted and the total amount of the ion in soil is accessible to plants (Jungk and Classen, 11997). Nutrients of low mobility, though, will be depleted only close to the root itself as is shown for Rb, as a tracer for K, in **Fig. 4**. Therefore, only a small portion of the chemically available K, i.e. exchangeable and interlayer K, is actually accessible to the plant. It can also be seen that the more roots a plant has, the more K can be taken up from soil.

The blackness of the soil or the shoots reflects the Rb concentration. The lighter color next to roots is due to Rb uptake that was translocated to the shoot. Black root tips show an accumulation of Rb that was taken up in older parts of the root.

Fig. 4: *Autoradiogram of oilseed rape seedlings in a soil labelled with ^{86}Rb.*

Distance from root, cm

Fig. 5: *Rb-depletion profiles of maize roots at the interfaces with soils of different texture (from Claassen et al., 1981).*

Figure 5 shows the depletion of Rb around maize roots growing in three soils differing in clay content (the clay mineral was of the 2:1 type). The soils had received 5 µmol Rb g^{-1} soil. It can be seen that in the sandy soil from Herrenhausen the degree of depletion at the root surface is higher and the extension of the depletion zone is wider.

The higher degree of depletion in the sandy soil is due to the fact that less Rb moved into the interlayer space and therefore, a larger proportion stayed readily available. The larger extension of the depletion zone clearly shows that Rb was more mobile in the sandy than in the loamy soils. These results show that in the sandy soil, more of the added Rb could be taken up by maize because a larger proportion stayed chemically available as shown by the higher maximum depletion at the root surface and furthermore, the mobility of this Rb was higher, as shown by the wider zone of Rb depletion. A more basic approach to nutrient movement in soil follows.

Usually only a small portion of the K taken up by plant reaches the root by mass flow (Jungk and Claassen, 1997) but diffusion is the dominant mechanism of K transport to roots. Diffusion is the process by which substances move from higher to lower concentration, i.e. along a concentration gradient. According to Fick's first law, (Eq. 1), the flux by diffusion, F_D, i.e. the amount of ions or molecules crossing a unit area per unit of time, is proportional to the concentration gradient, $\mathrm{D}C/\mathrm{D}x$, of the substance.

$$F_D = -D_e \frac{\mathrm{D}C}{\mathrm{D}x} \qquad (1)$$

The term C is the concentration of all ions per unit volume of soil that participate in diffusion. These include ions in the solution plus those ions on the solid phase that may be released into the soil solution, like the exchangeable and part of the interlayer K. The effective diffusion coefficient is D_e. It includes all factors that affect diffusibility in soil as compared to that in water. It is assumed that diffusion of ions in soil occurs in the soil solution only and so D_e can be expressed by the following formula (Nye, 1966):

$$D_e = D_L \, q f \, \frac{1}{b} \qquad (2)$$

D_L is the diffusion coefficient in water, q is the volumetric soil water content, i.e. the fraction of soil through which diffusion can take place, f is the impedance or tortuosity factor that takes into account the tortuous soil pore system through which diffusion occurs and b is the buffer power defined by Eq. (3):

$$b = \frac{DC}{DC_L} \tag{3}$$

C_L is the concentration of the ion in solution and so, in a simplified way, 1/b gives the proportion of diffusible ion that actually moves by diffusion.

The effective diffusion coefficient, D_e, is a measure of the mobility of an ion in soil. At the same concentration gradient, the higher is D_e the higher will be the flux by diffusion, F_D. Also the higher the mobility, i.e. D_e, the higher will be the extension of the depletion zone, D*x*, around roots. It can be estimated by Eq. 4 (Syring and Claassen, 1995):

$$Dx = \text{Ö}\ p\ D_e\, t \tag{4}$$

Equation 4 calculates the extension, D*x*, at 20 % of depletion. Now we can treat the extension of the depletion zone in Fig. 5 in a more quantitative way (**Table 2**).

Table 2 shows that the heavier soils Buelten and Bruendeln have a higher water content which favours diffusion but because of the higher clay content and a much higher buffer power which reduces ion mobility. This results in a much lower diffusion coefficient, De, and a lower extension of the depletion zone, D*x*. The calculated D*x* of 0.18 to 0.35 is well in the range of observed values showing that the basic principles of ion diffusion in soil properly describe K behaviour in the soil-root system.

From the preceding we can recognize that plant availability of soil K depends on two properties, i.e. quantity of available K and mobility of K in soil.

Table 2: Calculation of the extension of the depletion zone, D*x*, of figure 5, based on Eq. (4) and the components of the effective diffusion coefficient, D_e, Rb diffusion coefficient in water, D_L, volumetric soil water content, q, impedance factor, f, and the buffer power, b. Time of Rb uptake or time of diffusion was 3 days (Claassen, 1990)

Soil	DL 10^{-5} cm^2 s^{-1}	q cm^{3}m cm^{-3}	f	b	D_e 10^{-7} cm^2 s^{-1}	D*x* cm
Buelten	1.98	0.29	0.38	55	0.4	0.18
Bruendeln	1.98	0.29	0.38	19	1.1	0.30
Herrenhausen	1.98	0.24	0.28	9	1.5	0.35

A further aspect of plant availability of K in soil is related to the effect of root exudates (see **Fig. 2**). If root exudates are able to transfer part of the exchangeable or interlayer K into the soil solution, K transport to the root will be increased. Therefore, the type of K binding in soil, i.e. whether root exudates can mobilize it, is part of the concept of plant availability of soil K.

Potassium uptake efficiency of plants

Figure 1 showed that in the same soil, i.e. at the same K availability, K uptake differed greatly among crops, varying from 80 kg ha^{-1} for potato to 270 kg ha^{-1} for sugar beet. To analyse these differences in uptake, U, we may write equation (5):

$$U = RL \times In \times t \qquad [5]$$

Where RL is the length of the root system, In is the net influx and t is the time during which uptake takes place. Equation 5 is simplifying the system because RL varies with time as well as In but it makes clear which parameters to look at. Plants that grow for a longer period of time like winter crops as compared to summer crops (e.g. winter wheat and spring wheat) and more so perennial crops usually put less strain on the root system because there is more time to absorb the nutrient. In the following, we will concentrate on the size of the root system, RL, and on the net influx, In.

Size of the root system

The size and distribution of plant roots may vary greatly. Claassen and Steingrobe (1999) reported from several sources that total root length varied from 4 km m^{-2} for kohlrabi to 36 km m^{-2} for wheat. The latter reached down in the profile to 180 cm while spinach and kohlrabi only reached down to 60 cm. To relate the size of the root system to K uptake we will show the development of the root system of wheat and sugar beet shown in **Fig. 1**.

Figure 6 shows that sugar beet had only half the roots of wheat but even so absorbed 75 % more K than wheat (see **Fig. 1**). This shows that sugar beet roots were much more efficient in absorbing K from a K fixing soil than wheat roots. But before analyzing the K influx we will look at the effect of low K supply on root and shoot development.

Wheat, potato and sugar beet were grown in flowing solution culture

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Fig. 6: *Root length of spring wheat (SW) and sugar beet (SB) 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*

with K concentration varying from very low 1.5 µM to sufficient. **Table 3** shows the root/shoot ratio at optimum and low concentration.

Table 3: The effect of the K solution concentration on the root growth in relation to shoot growth expressed by the root/shoot ratio (Trehan and Claassen, 2000)

K concentration µM	Root/Shoot ratio		
	Potato $m\ g^{-1}$	Wheat $m\ g^{-1}$	Sugar Beet⁽²⁾ $m\ g^{-1}$
Optimum⁽¹⁾	68	98	130
1.5	38	150	152

(1) Optimum K concentration for wheat and sugar beet was between 5 and 15 µM, and for potato 50 to 200 µM.
(2) Unpublished data

It can be seen that potato having the lowest root/shoot ratio which even decreased at low K supply while in wheat and sugar beet there was rather a tendency for an increase. This negative reaction of potato to low K supply is together with its smaller root system is one reason for its low K uptake efficiency as shown in **Fig. 1**.

Potassium influx

The influx is the amount of nutrient taken up per unit of root and unit of time, e.g. mol cm^{-1} s^{-1}. At limiting soil K supply, it is a measure of the efficiency of the root to extract K from soil. In the prior section, it was seen that sugar beet had a smaller root system than wheat but absorbed 75% more K. This can only be explained by a higher uptake activity of each single root, i.e. by the influx. **Fig. 7** shows that sugar beet roots had a 7 times higher K influx than wheat at limiting soil K supply. The influx of sugar beet at no K fertilization was even much higher than that of wheat at high K supply. This means that if wheat roots had been as efficient as those of sugar beet its yield would have been maximum at no K fertilization.

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Figure 7: *Potassium influx of spring wheat (SW) and sugar beet (SB) grown on a sandy clay loam in the field with (+K) and without (-K) fertilization; n.s. no significant difference (p= 0.05) between (+K) and (-K) treatments; *significant differences (p= 0.05) between (+K) and (-K) treatments*

Trehan (2000) found that the higher K efficiency of potato variety Kufri Chandramukhi was not because of more roots but because the K influx was twice that of the K-inefficient variety Kufri Badshah. This shows that the K influx at the same soil K supply may vary greatly and that the influx is an important factor of the K efficiency of a plant.

The question that arises is how can the K influx in the same soil vary from one plant or root to another even though the availability is the same. The influx is the transport from outside of the root, i.e. the root surface, to inside of the root and it has to be equal to the transport from the soil to the root surface. The equations (diffusion being the main transport mechanism) governing the process of transport were shown before (Eqs. 1 to 4). The two components of the transport to the root (Eq. 1) are the concentration gradient, DC/Dx, and the effective diffusion coefficient, De. The concentration gradient could be influenced by the plant because DC is the concentration difference between the bulk soil and the root surface (see **Fig. 5**).

If a plant can decrease the concentration at the root surface to a low value and still have a high influx it will be able to create a steep concentration gradient and thereby a high flux to the root surface. The relationship between influx and concentration is described by the uptake kinetics.

The effective diffusion coefficient, De, might be considered as a property of the soil, but if, for example, root exudates displace K from exchange or interlayer sites (**Fig. 2**) the K concentration in soil solution will increase. Equation 3 shows that if the amount of available K, stays constant but a larger proportion of it is in solution, will increase and the buffer power decreases. And according to Eq. 2 the diffusion coefficient increases and thereby the mobility of K in soil. Therefore, if root exudates like H^+ or organic compounds displace K from the exchange sites, K transport to the root will increase.

In the following we will look at the uptake kinetics of plants grown in solution culture or in soil. The effect of root exudates will be estimated by model calculations.

Uptake kinetics

Wheat, sugar beet and potato were grown in flowing nutrient solution at 1.5, 5, 15, 50 and 200 µM K (Trehan and Claassen, 1998; Steingrobe and Claassen, 2000). Large tanks with nutrient solution and a continuous addition of K to the solution allowed for maintaining even a constant low K concentration. Wheat and sugar beet reached maximum yield at 5 µM K but potato needed 50 µM K.

The relationship between the average influx and the K concentration in solution is shown in **Fig. 8**. This relationship can be described by a modified Michaelis-Menten kinetic (see equation in the graph). I_{max} is the maximum influx extrapolated to infinite concentration, C_{Lmin} is the concentration at which net $I_n = 0$ and K_m is the Michaelis constant, i.e. the concentration at which $I_n = 0.5\ I_{max}$ minus C_{Lmin}. The higher is the Km, the lower is the efficiency of the root to absorb K at low K concentration.

It can be seen that at 1.5 µM and 5µM K wheat and sugar beet had a similar influx but potato only showed about one third of that value. This indicates that potato in soil would not be able to decrease the K concentration at the root surface to the same low value as the other species and therefore, the concentration gradient towards potato roots would be less than to wheat or sugar beet. This would mean a lower flux by diffusion, F_D, (see Eq. 1).

Fig. 8: *Average K influx, In, of sugar beet, potato and wheat grown in flowing nutrient solution at different K concentrations. The curves for describing these relations were calculated by a modified Michealis-Menten equation (see text).*

Wulff (1996) and similarly Claassen (1990) studied the uptake kinetics of plants grown in the field. Wulff (1996) found that rye had a much smaller Km value (30 to 100 µM) than sugar beet (800 µM) or potato (500 µM) and was therefore more K efficient. Notice the large difference in the absolute values between the shown solution experiment and the field conditions.

Model calculations

Model description: The model simulates nutrient desorption and transport in soil to the root surface and its uptake into the root.

Transport of nutrients to the root is by mass flow, FM, and diffusion, FD, (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 9** shows the major processes involved in nutrient transport and

Fig. 9: *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)*

uptake. In the first step, plants take up nutrients according to Mechaelis-Menten kinetics (**Fig. 8**), and water according 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

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

D_e = effective diffusion coefficient, $cm^2\ s^{-1}$ (see Eq. 2)

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

Total nutrient flux, FT to the roots is the sum of mass flow and diffusion

$$F_T = F_M + D_F$$

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:

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

D_L = diffusion coefficient in water

f = impedance factor

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 equation develops a mathematical model which enables calculating K uptake and K dynamics in the rhizosphere (Claassen, 1990; Jungk and Claassen, 1997; Claassen and Steingrobe, 1999; Steingrobe and Claassen, 2000).

The fourth process affecting nutrient transport and uptake (**Fig. 9**) 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 microorganisms and/or their exudates (Marschner *et al.*, 1986).

Table 4 shows the parameters used in the model calculation. The soil parameters are related to the ion mobility and transport in soil. The plant parameters relate to the uptake kinetics and to the geometry (root radius).

Table 4: Parameters used in calculation for no K fertilizer, June 24th – July 8th

	Wheat	*Sugar beet*
Soil parameters:		
D_L, diffusion coefficient in water, 10^{-5} cm^{-2} s^{-1}	1.98	1.98
q, vol. Water content, cm^3 cm^{-3}	0.40	0.36
f, impedance factor	0.22	0.18
b, buffer power	1569	1114
C_{Li}, initial soil solution concentration, 10^{-9} mol cm^{-3}	2.84	4.54
Plant parameters:		
I_{max}, maximum influx, 10^{-12} mol $cm^{-2}s^{-1}$	4.13	21.9
K_m, Michaelis constant, 10^{-9} mol cm^{-3}	9.7	6.6
C_{min}, minimum concentration, 10^{-9} mol cm^{-3}	0.5	0.5
r_o, root radius, 10^{-2} cm	1.2	0.9

Observed and calculated K influx

Model calculations were performed to see whether the knowledge we have about K availability in soil and K uptake by roots is sufficient to explain actual K uptake. If the model were to describe the differences in K influx of wheat and sugar beet as observed earlier (**Fig. 7**), then we would be able to find the reasons for those differences. **Figure 10** shows that the calculated K influx of wheat in June was close to the measured one but in July it was almost three times higher. For sugar beet the measured influx was always much higher than the calculated one and at the time of maximum K uptake, in July, measured influx was about 10 times higher than the calculated influx. This shows that the simulation model can not explain differences in K influx between wheat and sugar beet.

Said in a simple manner: at time of maximum K uptake our knowledge on the plant-soil system only explains 10% of K uptake.

Model calculation also allows for describing relationships that are difficult to measure directly. **Figure 11** shows such a case, i.e. the concentration profile around single roots of sugar beet and wheat. It can be seen that the concentration in solution decreases at the root surface to around 0.5 µM and is thereby already close to the minimum concentration, C_{Lmin}, (**Table 4**). The extension of the depletion zone is around 1 mm. This narrow zone of depletion

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Fig 10: *Comparision between measured and calculated K influx of wheat and sugar beet grown on a sandy clay loam in the field without K fertilization.*

Fig. 11: *Calculated concentration profiles of K in soil solution around the roots of sugar beet (dotted line) and wheat (continious line) grown on a sandy clay loam soil in the field in the period June 24th – July 8th.*

is due to the high buffer power which results in a small De and therefore small (Eq. 4).

Sensitivity analysis

A sensitivity analysis consists of changing only one parameter at a time and analyzing the change it causes in K influx. Thereby the significance of that parameter can be assessed for the conditions of the experiment under consideration. In this experiment the sensitivity analysis was done for two reasons: 1) to check whether a wrongly used parameter was the reason for the discrepancy between calculated and measured influx value and 2) which parameter may have changed in the rhizospere due to the action of the root to explain the higher measured than calculated influx value.

Of the plant parameters that are uncertain in plants grown in soil are those of the uptake kinetics. Mainly at limiting K supply I_{max} may increase (Claassen and Barber, 1976; Meyer, 1993). **Figure 12** shows that increasing I_{max} even by a factor of 10 had almost no effect on the calculated influx.

Fig. 12: Sensitivity analysis for sugar beet and wheat grown on a sandy clay loam in the field in the growth period June 24th - July 8th.

This can be explained by considering **Fig. 11** which shows that already with the "normal" I_{max} the concentration at the root surface dropped to a very low value and thereby the maximum concentration gradient toward the root developed. Even if the root required more K (higher I_{max}) the concentration gradient could not be enhanced and the transport to the root stayed unchanged. A decrease in Km would have a similar effect as increasing I_{max}.

Of the soil parameters, the concentration in soil solution can be determined quite accurately but the buffer power is rather uncertain because for it we need the diffusible K. Sometime the exchangeable K is taken but it is well known that part of the interlayer K also participates in the K supply to plants. Therefore we increased the buffer upto a factor of 10. Increasing the buffer power at constant C_{Li}, i.e. in Eq. 3, means increasing , i.e. the amount of diffusible K. It can be seen (**Fig. 12**) that changing the buffer power increased the K influx only slightly. From these results it is rather unlikely that the higher measured and calculated values can be explained by wrongly estimated parameters.

The hypothesis is that root exudates may increase the concentration of K in soil solution, C_{Li}. Therefore C_{Li} was changed and, as can be seen, K influx increased proportionally to C_{Li}. It can also be seen that C_{Li} should be increased by a factor 2 in wheat and a factor 10 in sugar beet in order to reach the measured K uptake. This is an indication that the high K influx of sugar beet is due to K mobilizing root exudates. Claassen and Trehan (1998) found that root exudates of potato, wheat and sugar beet increased the K concentration in a soil-root-exudate suspension, but the effect was relatively small. It therefore remains a major topic to be investigated what enabled mainly sugar beet to attain such a high K influx in this soil of very low K supply with K "fixing" clay minerals.

Conclusions

Potassium efficiency on a K fixing soil was lowest for potato followed by wheat and sugar beet. Potato had a similar total K requirement as wheat but because of fewer roots and less efficient uptake kinetics, K uptake was strongly reduced at low K supply. Wheat and sugar beet were similarly K efficient. Wheat had a lower K requirement than sugar beet and more roots, therfore, a small influx was sufficient. Sugar beet had a high K requirement and fewer roots but because of a high K influx it was equally K efficient. The high K influx was probably possible because of K mobilizing root exudates.

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