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Calculation of K Uptake by Three Crops Grown Under Controlled Conditions Using a Mechanistic Model

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Abstract: The aim of this study was to compare simulated and actual K uptake by three crops, under different K concentrations in the soil solution, in order to try to explain the underlying mechanisms of nutrient uptake by these crops. In 2002, wheat *(Triticum aestivum* L. cv. Star), barley *(Hordeum vulgare* L. cv. Madras) and sugar beet *(Beta vulgaris* L. cv. C+ T) were grown on a sandy clay loam, with various K concentrations in soil solution, in the growth chamber at the Institute of Agricultural Chemistry, University of Goettingen, Germany. Data were collected on K transport in soil and uptake by the three crops and used for simulation by a mechanistic model which encompasses uptake by root hairs as well**.** To quantify the significance of single soil and plant parameters for nutrient uptake, a sensitivity analysis was carried out. Under sufficient K in the soil solution, 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 wheat and barley 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 processes more than was considered by the model took place.

Key words: Mechanistic model; uptake kinetics; sugar beet; wheat; barley

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INTRODUCTION

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 in improving our understanding of the processes governing soil supply and plant uptake of mineral nutrients. Mechanistic models (Nye and Marriott 1969; Claassen and Barber 1976; Cushman 1979; Claassen *et al.* 1986; Claassen 1990) 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). They 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 the 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).

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) and 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 K efficiency of wheat, barley and sugar beet was investigated under controlled conditions (El Dessougi *et al.* 2002). It was shown that wheat, barley and sugar beet are K efficient species. Sugar beet efficiency was attributed to a very high net influx, whereas that of wheat and barley 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 the plants, under the experiment's conditions, were simulated by a mechanistic model.
The aim of this study was to compare simulated and actual K uptake of three plant species, under different K concentrations in the soil solution, in order to try to explain the underlying mechanisms of nutrient uptake by these species.

MATERIALS AND METHODS

Soil and plant parameters for calculating K uptake were obtained from a pot experiment under controlled conditions. The experiment was conducted in Anglberg sandy clay loam soil, having pH of 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 70% relative humidity. The photosynthetic active radiation during the day time was 250 $\mu E\ m^{-2}\ S^{-1}$. Four K levels: 0, 0.6, 2.4 and 4.8 g kg^{-1} soil were added as KCl. These fertilization 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 un- planted as control for measurement of soil parameters. The treatments were replicated three 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, potassium content of shoot dry

matter, root length (RL), mean root radius (r_0) the average half distance between neighbouring roots (r_l), K concentration in soil solution (C_{Li}), exchangeable K and the K influx were determined (El Dessougi *et al*. 2002).

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 volumetric water content (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 parameter could explain the discrepancy between calculated and measured K uptake, a sensitivity analysis was carried out. Each time only one parameter was changed, while all other inputs were kept constant. The soil parameters used in the sensitivity analysis in the pot experiment were C_{Li} and the buffer power of the soil (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.

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).

There are four processes involved in nutrient transport and uptake. The first process is that plants take up nutrients according to Michaelis-Menten kinetics and water due to transpiration. If nutrients transported by mass flow are less than those taken up by the root, the concentration at the root surface decreases, establishing concentration gradients around the roots. The second process is transport to the roots along the concentration gradients. Decreasing the concentration of the soil solution, through K uptake by plants, disturbs the equilibrium between K ions sorbed to the

soil solid phase and dissolved ions in soil solution. This leads to the third process; 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). Because of mass conservation, total 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. The fourth process in nutrient transport and uptake processes is chemical mobilization of nutrients by root exudates.

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 (mol cm^{-3})

b: Buffer power defined as the ratio of the changes in diffusible K due to fertilization to soil solution concentration (dC/dC_{Li}). For example, the addition of 20 umol K per cm^{-3} soil increased exchangeable K by 0.6 umol per cm^{-3} soil and C_{Li} by 0.014 umol per cm^{-3}. This resulted in a buffer power (b) of 43.

D_L: The diffusion coefficient of K in water at 25°C (1.98×10^{-5}) cm^2 s^{-1} (Pearson 1966).

Θ: Volumetric water content of the soil (cm^3 cm^{-3})

f: Impedance factor (f =0.97 8-0.17) (Kaselowsky 1990)

V_0: Water influx calculated by dividing the transpiration rate by the root surface area (cm^3 cm^{-3} s^{-1}).

Root Parameters

(i) Uptake kinetics:

I_{max}: Maximum influx theoretically achieved at infinite concentration (mol cm s^{-1}). The I_{max} values 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 fertilization, in the pot experiment, was 10.5 x 10^{-14} mol $cm^{-1}s^{-1}$. At a C_{Li} 5 µmol, 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 value was multiplied by factor 1.2, a factor reported by the author for wheat at a comparable C_{Li} of around 2.3 umol mol cm^{-1} s^{-1}solution

K_m: Michaelis constant is the concentration that allows uptake at half l_{max} - C_{Lmin} (mol cm^{-3}).Values were taken from Meyer (1993)

C_{Lmin}: Minimum solution concentration at which influx equals efflux or net influx equals zero (mol cm^{-3}). Values were taken from Meyer (1993)

(ii) Geometry:

r_0: Root radius, determined as described by El Dessougi *et al*. (2002)

r_1: Average half distance between neighbouring roots

RL_1: Root length at first harvest

k: Growth rate constant of roots

(iii) Root hairs

N: Number of root hairs per centimetre root

r_1h: Average half distance between neighbouring root hairs

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. The calculated influx was obtained by dividing the total uptake by the average root length and time.

RESULTS

The results of the pot experiment 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.

The measured K influx of the three crops 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. 1a and Fig. 2a). At the highest C_{Li} of 2.65 mM, calculated and measured influxes for the three species were similar, i.e. the actually measured influx was closely predicted by the model (Fig. 1a). As indicated by the flat concentration curves (Fig. 1b), 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. 1b).

Figure 2a 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 2b 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. 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 (ΔCd) 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. The extension of the concentration profiles of the three crops 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. 2b).

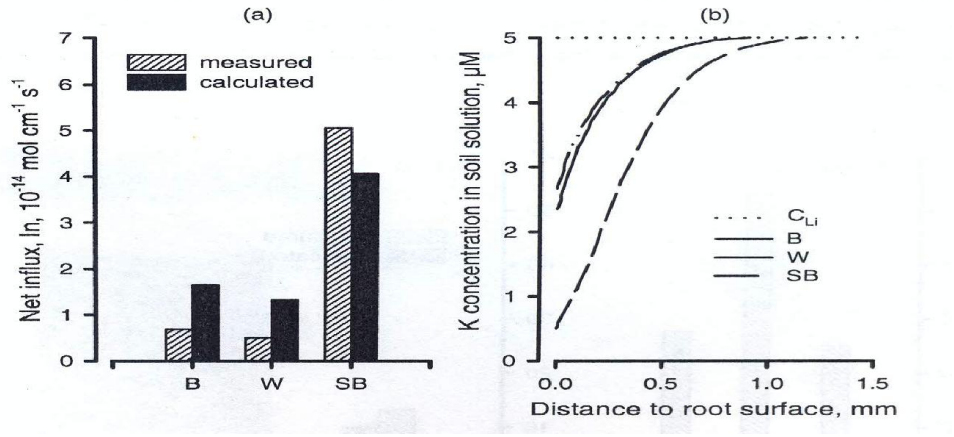

Figure1. (a) Measured and calculated K influx of barley (B), wheat (W) and sugar beet (SB) grown on a sandy clay loam at 2.65 mM K concentration in soil solution, and (b) calculated concentration profiles of K in soil solution around the roots after 10 days of K uptake

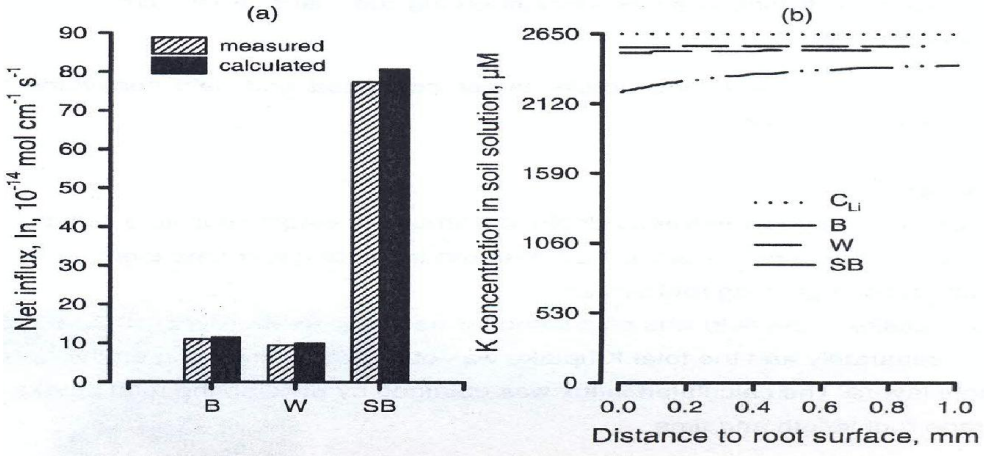

Figure 2. (a) Measured and calculated K influx of barley (B), wheat (W) and sugar beet (SB) grown on a sandy clay loam at 5µM K concentration in soil solution, and (b) calculated concentration profiles of K in soil solution around the roots after 10 days of K uptake

Figure 3 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. The 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.

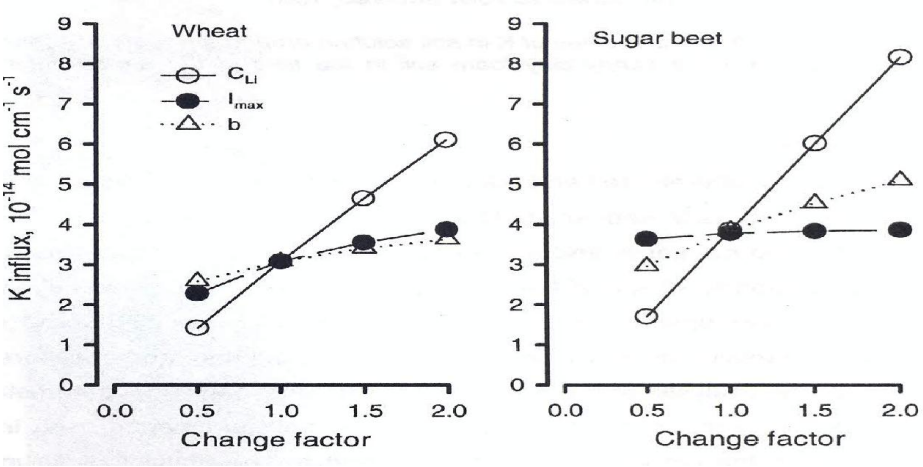

Figure 3. Sensitivity analyses for sugar beet and wheat grown under controlled conditions at 5µM K concentration in soil solution

The concentration profiles presented in Fig. 2b show that wheat decreased the concentration at the root surface (C_{L0}) 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 the 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.

The results of the sensitivity analysis for wheat and sugar beet at a C_{Li} of 2.65 mM are shown in Figure 4. Here the situation was completely reversed, where it is clear 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.

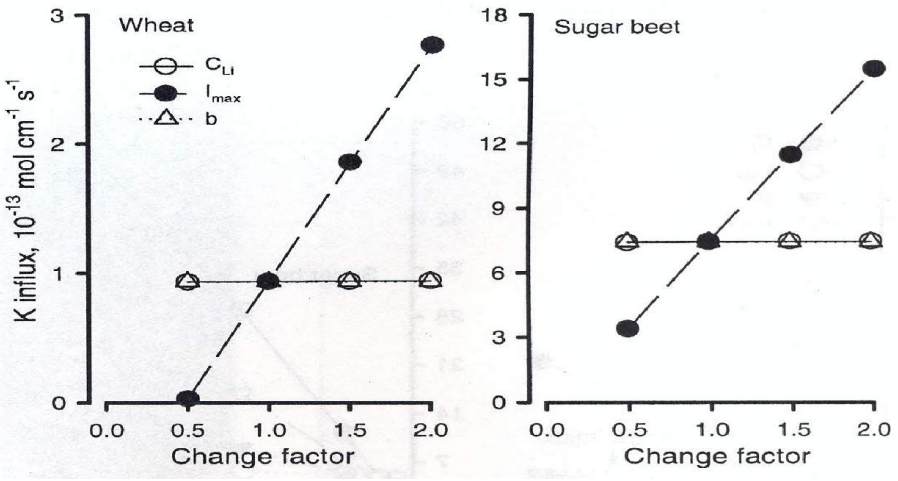

Figure 4. Sensitivity analyses for sugar beet and wheat grown under controlled conditions at 2.65mM K concentration in soil solution

DISSCUSION

Potassium uptake was calculated realistically by the model in some cases, while in others calculated K uptake was either over- or under-predicted by the model. 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). The model simulated the measured uptake accurately at the highest fertilization level with a C_{Li} of around 2.65 mM. 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 shown by the larger extension of the depletion zones, due to the smaller b value, 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 K concentration in the soil solution, the model was unable to estimate the measured K influx of the three plant species. For the cereals, the calculated as compared to measured uptake, was nearly thrice higher at this low C_{Li} value. Potassium concentration at the root surface was not decreased to a minimum value; hence, transport was not the only problem but also the uptake kinetics. For 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 processes besides desorption, diffusion and mass flow took place. The concentration profiles showed that both cereals did not decrease the C_{L0} to minimum values and thus the maximum concentration difference was not established indicating low transport to the roots. 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 showed that at a C_{Li} of 5µM, I_{max} had a greater influence on calculated K uptake of wheat. 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}. They 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 seen why K deficient plants were not able to increase I_{max}, since as was seen in K fertilized plants, higher l_{max} values could be established.

To achieve the much higher measured influx than the cereals, sugar beet needed a much greater ΔC_L. This was possible by decreasing the concentration at the root surface further (down to 0.5µM) than the cereals. The resulting concentration gradients were steeper and also maximum K flux to the roots was achieved. Thus, increased uptake capacity of the roots such as higher I_{max} did not enhance uptake, because 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 Claassen (1994) and Steingrobe and Claassen (2000), the higher the C_{Li} the greater is the possible concentration difference (ΔC_L) between the bulk soil and the root surface. 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}. It could be concluded that higher calculated influx could be achieved only by using a higher value for C_{Li} in modelling.

Increasing the buffer power (b) did not have great influence on calculated K influx, where doubling the b value increased calculated influx of wheat and sugar beet just by 11% and 13%, respectively. The effect of b was greater than that reported by Claassen (1994) who found that increasing b by a factor of 10 brought a negligible increase in calculated K influx when no root competition for K existed. He simulated K uptake without taking uptake by root hairs into account, whereas the simulation in the present 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, the gradient in solution ($\Delta C_L/\Delta X$) rather than the gradient of available nutrients ($\Delta C/\Delta X$) is the deciding factor for diffusion. Since the relation between both gradients is described by the buffer power, they 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, 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.

The results 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. Thus, the model described the uptake correctly. On the other hand, sugar beet had a higher influx which could only be explained by the model, 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.

CONCLUSIONS

1. At high soil solution concentration, transport by mass flow and diffusion does not limit uptake, and K influx is determined by l_{max}.
2. The correct prediction of the measured uptake of cereals by the model means that their large root system and accordingly the smaller needed influx were the reason for the K efficiency.
3. 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}.

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حساب إمتصاص البوتاسيوم لثلاثة محاصيل تحت ظروف متحكم بها بإستعمال أنموذج حسابي

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المستخلص: هدفت هذه الدراسة لمقارنة القيمة الفعلية والقيمة المحسوبة لإمتصاص البوتاسيوم بواسطة ثلاثة محاصيل، تحت تركيزات مختلفة من البوتاسيوم في محلول التربة، وذلك فى محاولة لتفسير آليات إمتصاص العناصر الغذائية بواسطة هذه المحاصيل. فى عام 2002 زُرع القمح (الصنف ستار) والشعير (الصنف مدراس) وبنجر السكر (الصنفC+T) في تربة طمية رملية طينية وفي وجود تركيزات مختلفة من البوتاسيوم، في حجرة نمو بمعهد الكيمياء الزراعية جامعة قوتنقن بالمانيا . جُمعت بيانات عن انتقال البوتاسيوم في التربة وإمتصاصه بواسطة المحاصيل الثلاثة واستُخدمت في محاكاة (Simulation) بأنموذج حسابي يشتمل على امتصاص البوتاسيوم بواسطة الشعيرات الجذرية. ومن أجل دراسة أهمية التأثير الكمي لخصائص التربة والنبات على امتصاص العناصر الغذائية أجرى تحليل حساسية النموذج. عندما كان تركيز البوتاسيوم في محلول التربة كافيا، ولم يكن الانتقال محددا للامتصاص، تمكن النموذج من تقدير الامتصاص الفعلي للبوتاسيوم بصورة دقيقة. أما عندما كان تركيز البوتاسيوم غير كاف في محلول التربة كانت القيم المحسوبة بالنموذج أعلى من القيم المحسوبة للقمح والشعير وكانت أقل من المتوقع لبنجر السكر. أظهر التركيز المحسوب حول الجذور أنه بالنسبة للغلال فان استعمال قيمة خاطئة لمعيار حركة إمتصاص البوتاسيوم أدى إلى القيمة الاعلى من المتوقع أما بالنسبة لبنجر السكر فقد تدخلت عوامل خارج نطاق النموذج.

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