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Calculation of K Uptake by Two Crops Grown under Field Conditions Using a Mechanistic Model

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Abstract: The objective of this study was to compare simulated and actual potassium uptake by two crops, using soil and plant parameters obtained from a field experiment conducted in 2003, in Bavaria, southern Germany. Sugar beet *(Beta vulgaris* L. cv. Kawetina) and wheat *(Triticum aestivum* L.cv. Star) were grown on a sandy clay loam in the field. The K transport in soil and uptake by the plants were simulated by a mechanistic model which encompasses uptake by root hairs as well**.** A sensitivity analysis was carried out in an attempt to understand the significance of single soil and plant parameters for nutrient uptake. The simulation model calculated only 34 % of the measured sugar beet uptake throughout the growing period. The lowest calculated K influx (only 9 % of measured value) corresponded to the period June 24th–July 8th of highest actual uptake. Sensitivity analysis showed that, under low K concentrations, K concentration in the soil solution was the most important factor controlling K uptake, especially for sugar beet. This indicates that roots may have increased the K concentration in soil solution by chemical mobilization. Research is needed to understand the mechanism by which this is achieved.

Key words: Mechanistic model; rhizosphere; sensitivity analysis; wheat; sugar beet

INTRODUCTION

Nutrient availability in the soil and plants ability to acquire nutrients is the basis for supplying plants with mineral nutrients (Jungk and Claassen 1997). Therefore, both soil and plant properties are important for plant nutrition. Nutrient availability encompasses the chemically available nutrients and their movement in the soil. The acquiring ability of plants is

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determined by the size of the root system and by morphological root characteristics such as root length, root radius and root hairs, and by physiological properties such as the uptake parameters (I_{max}, K_m, and C_{Lmin}) and exudation of solubilizing compounds, which, in turn, determine the uptake rate per unit root and time or the influx.

Plants change the chemistry of the rhizosphere by changing the pH through exudation of H^+, by roots exudates, which comprise both high and low molecular weight compounds and by interactions with micro-organisms and/or their exudates (Marschner *et al.* 1986). Chemical mobilization of nutrients in the rhizosphere by plant roots can substantially change the availability of, for example, phosphate and micro-nutrients (Cakmak *et al.* 1994; Beissner and Roemer 1998; Rengel *et al.* 1998).

Nutrient simulation mechanistic models enable us to calculate the nutrient uptake from soils, as affected by the involved soil and plant factors, and to quantify the significance of individual soil and plant parameters in the process (Claassen *et al.* 1986). They provide means of calculating not easily measurable data and 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 (Claassen and Steingrobe 1999).

The aim of this study was to compare simulated and actual K uptake of wheat and sugar beet, under different K concentrations in the soil solution, in order to try to explain the underlying mechanisms of nutrient uptake by these crops.

MATERIALS AND METHODS

Field experiment

The field data were obtained from a long-term fertilizer experiment on a sandy clay loam with a high K fixing ability having pH 7.2, 33 % clay, 31 % silt and 3.8 % organic carbon in Bavaria, southern Germany. The K fertilization rates varied from 0 to 1000 kg K ha^{-1} $year^{-1}$. These treatments were applied from 1976 till 1986. In 2003, wheat cultivar Star and sugar beet cultivar Kawetina were sown on 50 m^2 plots, on the 13th of March and 04th of April, respectively. Before sowing, 43 kg P $ha^{-1}$and 80 kg N ha^{-1} were applied to the soil. Harvests were carried out on 27th May, 24th June, 08th July, and 05th August for both crops and on 07th October for sugar beet. At each harvest date, 3 sub-samples of plants, roots and soil of each species were taken from random areas of the plots from the 0 kg K fertilized (-K) and highest fertilizer level of 1000 kg K ha^{-1} (+K) treatments. 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_1), K concentration in soil solution (C_{Li}), exchangeable K and the K influx were determined as described by (El Dessougi *et al.* 2011).

Model description

Figure 1a shows the four major processes involved in nutrient transport and uptake: nutrients uptake by plants according to Michaelis-Menten kinetics (Nielson 1972); transport to the roots along the concentration gradient governed by mass flow and diffusion (Barber 1962); desorption according to the buffer power (b) of the soil (Claassen and Steingrobe 1999; Steingrobe and Claassen 2000). The last process, i.e. chemical mobilization of nutrients by root exudates is not included in the model used in this research. Figure 1b shows the concentration profile of an ion in the rhizosphere as shown in Figure 1a.

Plant and soil parameters

The parameters of nutrients transport in the soil used for nutrient uptake simulation were the concentration in soil solution, buffer power, the diffusion coefficient, the volumetric water content of the soil, the impedance factor and the water influx.

The root parameters were the uptake kinetics and root geometry. The uptake parameters included: the maximum influx theoretically achieved at infinite concentration, the Michaelis-Menten constant and the minimum solution concentration at which influx equals efflux or net influx equals zero. Values were taken from Meyer (1993).

The root geometry were root radius, the average half distance between neighbouring roots, the root length at first harvest, the growth rate constant of roots (El Dessougi *et al.* 2011), number of root hairs per centimetre root and average half distance between neighbouring root hairs (Claassen 1994).

Model output

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

Sensitivity analysis

A sensitivity analysis was carried out to study the effect of the different parameters used in the model on the calculated K influx and uptake. Each time, only one parameter was changed while all other inputs are kept constant. The soil parameters used in the sensitivity analysis were C_{Li} and b, while I_{max} was chosen to study the effect of the root physiological uptake capacity on K uptake.

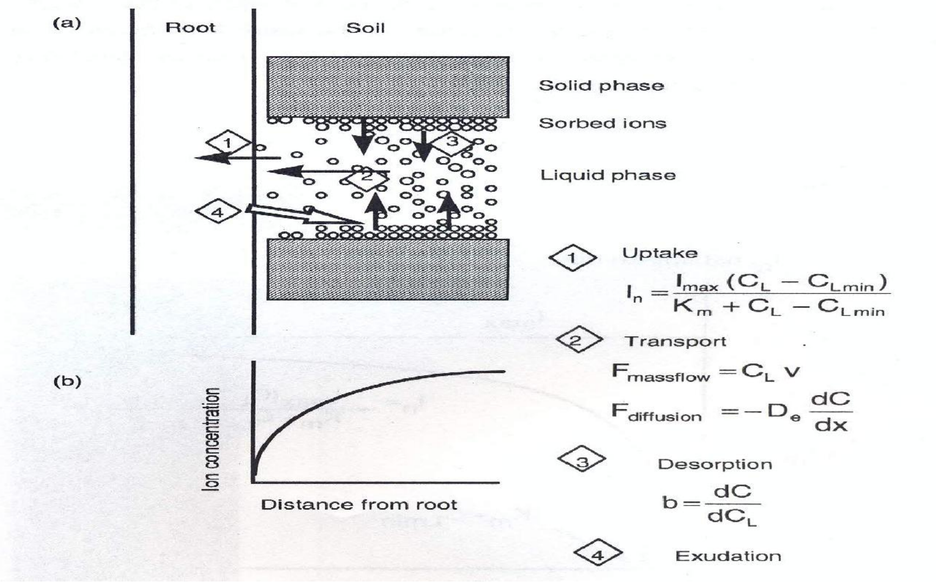

Figure 1. (a): The soil-root system consisting of the root surrounded by the soil solid phase with sorbed ions and the pore space filled with liquid . Circles symbolise ions; (b): concentration profile of an ion in the rhizosphere as shown in (a). Modified from Claassen and Steingrobe (1999**)**

RESULTS

Under sufficient K conditions the model calculated correctly the measured uptake in the fields of wheat and sugar beet (data not shown). It is more important to study the plant performance under deficient K conditions, hence, only the calculated uptake of plants from unfertilized treatments will be discussed here.

The calculated K influx for sugar beet was by far lower than the measured one; however, the degree of under-prediction of K influx by the model varied between the different growth periods (Fig. 2). Generally, the model calculated only 34% of the actually measured uptake, and the least calculated K influx was in the period June 24th–July 8th, 2003. It is interesting to note that it was, at this growth period, the highest actual uptake occurred. On the other hand, calculated and measured K influxes of wheat were more or less equal in the period May 27th–June 24th. In June 24th–July 8th, however, the model calculated only 40% of the actual K influx.

Sugar beet and wheat decreased the concentration at the root surface to about 0.5 µM, which corresponds to 12 % and 22 % of the actual C_{Li} of sugar beet and wheat, respectively. The respective ΔC_L were 4 and 2 µM. No root competition existed, since the concentration at r_1 reached the value of C_{Li} (Fig. 3).

The sensitivity analysis showed that, under field conditions, and for both crops, only a higher C_{Li} value would be effective in covering the gap between the calculated and measured influx (Fig. 4). The influence of C_{Li} on calculated influx was similar for the two crops; however, for sugar beet the discrepancy between measured and calculated influx was much higher. Hence, doubling C_{Li} value for wheat was enough to equalize calculated and measured influx, whereas the C_{Li} value for sugar beet had to be increased by factor 10 in order to achieve the same effect. Since both crops created the highest possible ΔC_L (Fig. 4) and as such maximum diffusive flux to the roots, an increased I_{max} or b would not improve the calculated uptake. Even by increasing both parameters by factor 10, the calculated influx was not equal to the measured one.

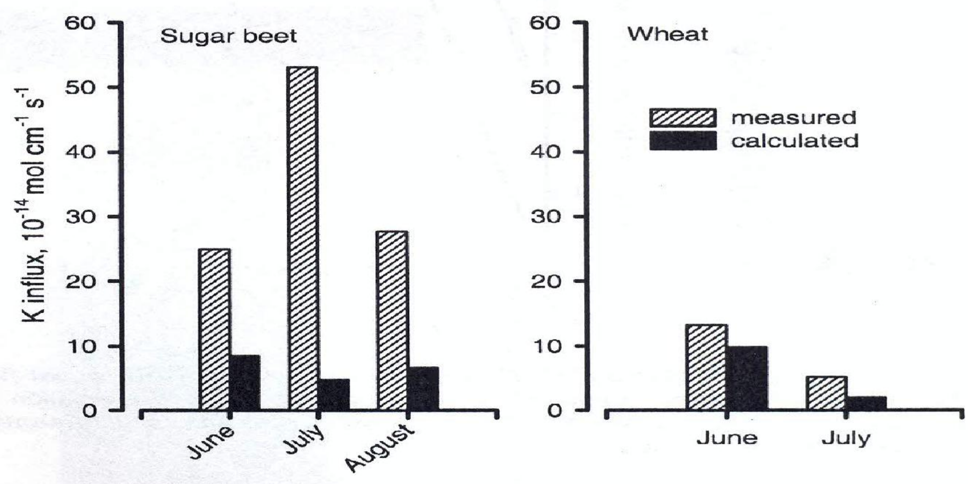

Figure 2. Measured and calculated K influx of wheat and sugar beet grown on a sandy clay loam in the field without K fertilization

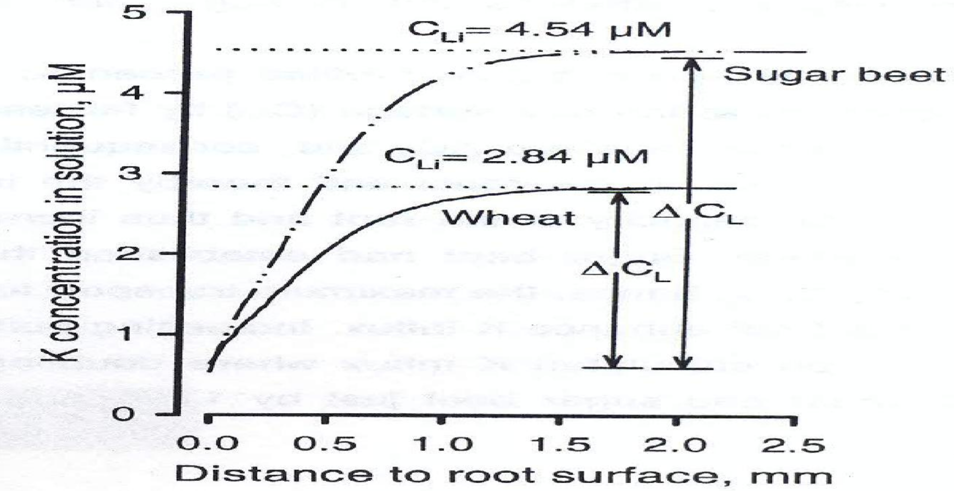

Figure 3. Calculated concentration profiles of K in soil solution around the roots of sugar beet and wheat grown on a sandy clay loam in the field

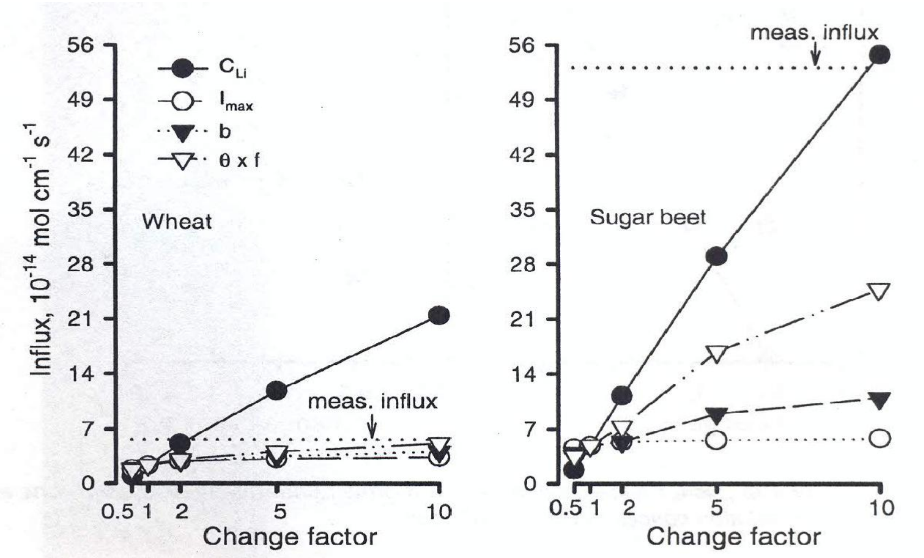

Figure 4. Sensitivity analyses for sugar beet and wheat grown on a sandy clay loam in the field

The diffusion path is through water-filled pores only, hence, Θ affects both the diffusion path and the diffusion cross-sectional area. At high volumetric water content (Θ), the diffusion path will be more direct than under low Θ conditions, where the ions will pass through a longer and more tortuous path, i.e. they will be met with higher resistance. This resistance is described by the impedance factor (f), where f is the inverse of the resistance. The combined influence of Θ x f on the calculated K uptake was evaluated, since changing Θ changes f, and the relation between both factors is nearly linear in the range of available water (Bhadoria *et al.* 1991). Since Θ and f describe the nature of the diffusion path, it is expected to be very influential on calculated K uptake. Influence of Θ x f on calculated K uptake, although greater than the influence of I_{max} and b, was, however, by far lower than that of C_{Li}. Increasing Θ x f by factor 10 helped to explain the discrepancy between calculated and measured influx for wheat, whereas that increased calculated uptake of sugar beet by 50 % (Fig. 5).

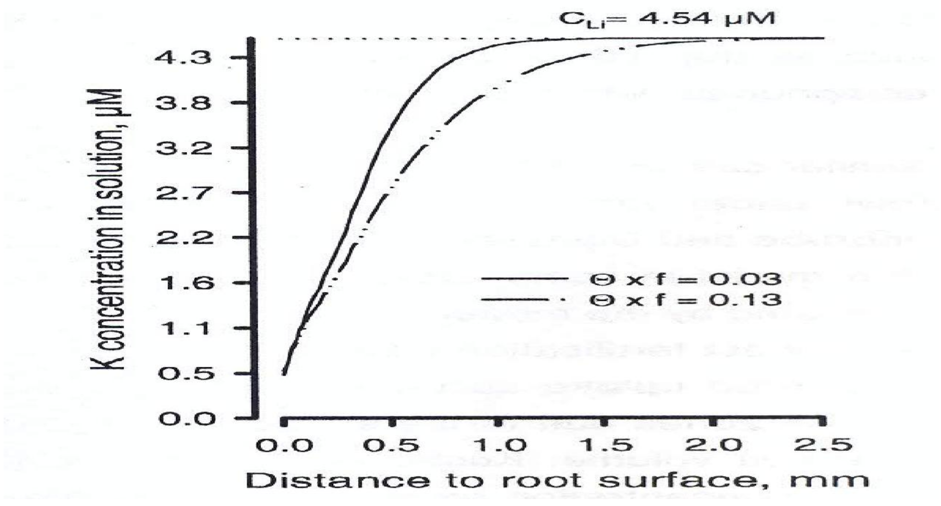

Figure 5. Calculated concentration profiles around the roots of sugar beet grown on a sandy clay loam in the field at low and high Θ x f conditions

In a dry soil, the diffusion coefficient (D_e) is small and the plant needs steeper gradients in order to increase the flux to the roots. This is possible through the smaller extension of the depletion zones in dry as compared to wet soil (Fig. 5). However, in dry soils nutrient mobility is by far much reduced resulting in low flux to the roots and accordingly uptake per unit root. Hence, the roots would not be able to improve the low transport encountered under dry soil conditions by decreasing C_{L0} to a lower value.

Using $F_D = -D_e.\frac{dC}{dx}$ - and for the extension of the depletion zones Δx $= \sqrt{\Pi D_e t}$, it can be shown that F_D is proportional to $\sqrt{\Theta f}$. This explains also the non linear function of Θ x f to the flux in comparison to the linear relation found between the soil solution concentration (C_{Li}) and the diffusion flux since $D_e = D_L \Theta f \frac{\Delta C}{\Delta x}$.

DISSCUSION

Calculated K uptake of wheat was only realistically estimated by the model in the period May 27th–June 24th 2003. It seems that the created ΔC_L was enough to provide the necessary concentration gradient needed to drive nearly the actually measured K flux to the roots. However, calculated K uptake was under- predicted by nearly 50 % in the period June 24th –July 8th and was very much under-predicted for sugar beet, especially in July, the time of highest K requirement. The results are in variance with those of Claassen (1994) who found similar calculated and measured K uptake by sugar beet, with and without fertilization, and under-prediction of K uptake for wheat in July in the unfertilized treatments only.

Both crops decreased the C_{L0} to around 0.5 µM, as was shown by the concentration profiles around the roots of wheat and sugar beet in the period June 24th–July 8th. Due to the higher C_{Li} on sugar beet plots, a higher ΔC_L was possible and, consequently, steeper concentration gradients and higher diffusive transport to the roots. Hence, sugar beet was able to achieve a higher influx in comparison to wheat. Nevertheless, the calculated influx of sugar beet, in the period 24 June – 8 July, was somewhat lower than that of wheat (Fig. 2). The calculated uptake was obtained by summing up the uptake from the single soil layers (0-90 cm). The K concentration in soil solution at the 15-30 cm was very low (1.43 µM); consequently, the calculated uptake in this layer was also low. This explains the observed discrepancy, since Figure 3 represents only the calculated concentration profiles in the soil layer 0-15 cm. It is interesting to note that in July, the period of highest demand for K, and although C_{Li} and ΔC_L were lower than in June and the actual uptake was highest, the model calculated the least (9 %) uptake.

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

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

The root physiological characteristics or the uptake kinetics (I_{max}, K_m, and C_{Lmin}) were not measured directly in the soil, as such the probability of inaccuracy is much higher by those factors. Claassen (1994) attributed the reduced K uptake by sugar beet in June to a very high K_m value, since the plants, even under K deficiency conditions, were unable to further decrease the concentrations at the root surface and, therefore, increase the K flux to root. However, when the transport in the soil is limiting uptake, improving K uptake kinetics such as increasing I_{max} or decreasing K_m and C_{Lmin} would not help in increasing calculated potassium uptake. This is because both crops created the highest possible ΔC_L and as such maximum diffusive flux to the roots, a higher I_{max} or b value would not influence the calculated K uptake. This is especially true for sugar beet, where the sensitivity analysis showed that increasing I_{max} by factor 10 resulted in only 11 % increase in calculated K uptake. Increasing I_{max} had a somewhat higher effect on calculated K uptake of wheat; nevertheless, a further decrease of C_{L0} to minimum concentrations would not be enough to explain a difference of 50% between calculated and measured uptake.

The reason for the observed discrepancy between the measured and the calculated uptake could be due to the fact that the model describes only sorption and transport of nutrients in the soil as well as uptake. However, it seems that the plants did influence the rhizosphere chemically, thereby increasing the nutrient availability. The increased nutrients availability had a similar effect to that of an increased C_{Li} in the model. The source of the larger amount of available K may be the non-exchangeable K. Meyer and Jungk (1993) explained the discrepancy between measured and calculated K uptake by including the release kinetics of the non-exchangeable K in the model. Whether the release of non-exchangeable K is due to some root exudates, such as organic acids or protons which exchange for K or some other phenomena, is not known.

An interesting observation is that the plants in the field were able to achieve a much higher influx as compared to those grown under controlled conditions (El Dessougi *et al*. 2002). Evidence exists that plant roots cause acidification in the rhizosphere by light dependent active excretion of H^+ (Mengel and Malissiovas 1982). Therefore, the higher light intensity in the field, as compared to the growth chamber, could be the reason for the higher K influx of plants grown in the field. The excreted H^+, probably accompanied by the release of organic anions, must be of vital significance for many reactions going on in the rhizosphere.

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

CONCLUSIONS

1. Higher calculated nutrient availability can be obtained by the model only if C_{Li} is increased.
2. Some processes which increase the availability of nutrients occur in the rhizosphere.
3. More research is needed to investigate the processes involved in increasing nutrient availability in the rhizosphere

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قياس إمتصاص البوتاسيوم بمحصولين تحت ظروف الحقل بإستعمال نموذج حسابي

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المستخلص: هدفت هذه الدراسة لمقارنة القيمة الفعلية والقيمة المحسوبة لإمتصاص البوتاسيوم لمحصولين باستخدام معايير (معلمات) التربة و النبات من تجربة حقلية أجريت عام 2003في باقاريا، جنوب المانيا. زرع القمح (الصنف ستار) وبنجر السكر (الصنف كافيتينا) في تربة طمية رملية طينية. تم حساب حركة انتقال البوتاسيوم وامتصاصه بواسطة النباتات بإستعمال نموذج حسابي يأخذ في الاعتبار امتصاص البوتاسيوم بالشعيرات الجذرية. أُجري تحليل الحساسية في محاولة لفهم أهمية خصائص التربة والنبات فى امتصاص العناصر الغذائية. تمكن النموذج من حساب 34% فقط من الامتصاص الفعلى لبنجر السكر طوال فترة النمو. كان أقل حساب لامتصاص البوتاسيوم في الفترة 24 يونيو-8 يوليو التي تم فيها أعلى امتصاص فعلي للبوتاسيوم. أ وضح تحليل الحساسية□ تحت ظروف حد النقص ان تركيز البوتاسيوم في محلول التربة كان أهم عامل متحكم في إمتصاص البوتاسيوم خاصة بالنسبة لبنجر السكر. هذا يبين ان الجذور قد تكون زادت تركيز البوتاسيوم في محلول التربة بالتحريك الكيميائي. هنالك حاجة لمزيد من البحوث لفهم الآلية التي تم بها هذا.

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