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Potassium availability in relation to soil moisture

II. Calculations by means of a mathematical simulation model

Kaliumverfügbarkeit in Beziehung zur Bodenfeuchte

II. Rechnungen mit einem Simulationsmodell

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Summary In order to study the influence of soil moisture on the availability of potassium a simulation model was used. The model is designed to describe the transport of a nutrient from the soil to plant roots and its distribution around a root. From a pot experiment, the measured K uptake of onion plants, grown in soil under different moisture levels, agreed satisfactorily with the calculated K uptake. The model is therefore regarded as a valid means of quantifying the dynamics of K in the soil around plant roots.

Calculations from a loess soil have shown that decreasing water content resulted in
– a strong decrease of K transport from the soil to the root,
– a faster decrease of the K concentration at the root surface and therefore
– increasingly steep gradients of the K concentration around the root

With the root density found in this experiment the K concentration of the moist soil ($\theta \sim 0.4$) decreased almost equally in the total soil volume whereas in the dry soil ($\theta \sim 0.1$) not much change occurred in the middle between two roots.

Therefore, the rate of K uptake per unit of root decreased much faster in the dry than in the moist soil. Calculations for sandy and loess soils, which have different water tension curves, have shown that the availability of K in the sandy soil is much more sensitive to changes in water tension than in the loess soil.

The simulation technique can thus be used to analyze the influence of single factors on the availability of K and to estimate the extent of this influence.

Zusammenfassung Um den Einfluss des Wassergehaltes des Bodens auf die Verfügbarkeit von Kalium zu untersuchen, wurde ein Rechenmodell angewendet, das den Transport eines Nährstoffs vom Boden zur Wurzel und dessen Verteilung in der Umgebung der Wurzel beschreiben soll. An einem Gefässversuch mit Zwiebelpflanzen bei unterschiedlicher Bodenfeuchte ergab die Rechnung eine befriedigende Übereinstimmung mit der gemessenen K-Aufnahme der Pflanzen. Daraus wird geschlossen, dass das Modell realistisch genug ist, um auch die K-Dynamik im wurzelnahen Boden zu quantifizieren

Solche Rechnungen haben an einem Lössboden gezeigt, dass abnehmendem Wassergehalt
– der K-Transport aus dem Boden zur Wurzel stark abnimmt,
– die K-Konzentration an der Wurzeloberfläche rascher sinkt, und daher
– zunehmend steilere K-Konzentrations-Gradienten in Wurzelnähe enstehen.

Bei der gegebenen Wurzeldichte sinkt die K-Konzentration des feuchten Bodens im gesamten Volumen nahezu gleichmässig ab, während sie im trockenen Boden in der Mitte zwischen zwei Wurzeln nur wenig abnimmt. Die K-Aufnahmerate pro Einheit Wurzel sinkt daher in trockenem Boden viel rascher als in feuchtem Boden ab. Rechnungen an Sand- und Lössböden, die sich durch ihre Wasserspannungskurve deutlich unterscheiden, zeigen sinngemäss, dass ein Sandboden in seiner K-Verfügbarkeit auf Änderungen der Wasserspannung viel empfindlicher als ein Lössboden reagiert.

Die Modellrechnung ermöglicht es demnach, die Wirkung einzelner Faktoren der K-Verfügbarkeit zu erkennen und in ihrem Ausmass abzuschätzen.

Introduction

Plant availability of potassium increases with increasing water content in soil. This has been demonstrated under field conditions by van der Paauw[12] and Barber[2]. Kuchenbuch *et al.*[8] have shown that low levels of soil moisture reduced both root growth and the rate of potassium inflow per unit of root length of onion plants. The mobility of potassium in the soil was decreased. It is therefore assumed that the water content of the soil influences the rate of potassium uptake by its effect on the transport of potassium from the soil to the root surface.

A direct quantitative measurement of the flux of potassium from soil to plant roots under natural growing conditions is not possible. An attempt has therefore been made to mathematically characterize the factors that determine both nutrient transport from the soil to plant roots and uptake by plants in order to simulate the whole process[4,6,11,13,15]. In this way it is also possible to quantify the influence of changing the size of one parameter on the soil-plant system as shown by Silberbush and Barber[16].

In this paper a simulation model of Claassen *et al.*[5] was used to study the influence of water content of the soil on the transport of potassium through plant roots. This model calculates the inflow of a nutrient per unit of root length within a given period of time and also the distribution of this nutrient in the soil around the root. The aim of the work is specifically

– to verify the model in regard to the influence of soil water content and

– to quantify the influence of individual factors on the availability of potassium – *i.e.* transport of K from the soil to the root, root growth, and soil texture.

Materials and methods

Soil

Top layer of Söderhof silt loam soil. Details are mentioned in part I of this paper[9].

Pot experiment for determining K uptake of plants

Onion seedlings were grown 19 days under equal conditions in special containers as described by Kuchenbuch *et al.* (submitted). Thereafter, volumetric water content was brought to different values between 0.1 and 0.4 cm^3 water per cm^3 soil and the plants grown for another 19 days under these conditions. Water content was replenished every day by weight. The first harvest was made after 19 days, the second after 38 days. Potassium content was measured in the above ground portion of the plants. The influence of water content on potassium uptake was determined by the difference of K uptake between the first and the second harvest.

Parameters for the simulation model

I_{max}, maximum rate of uptake was obtained from the pot experiment. As previously shown[9] the rate of K uptake levelled off with $\theta = 0.25$ in the soil used. By adding 10% to this value to insure a maximum rate, a figure of 2.9 p mol. cm^{-2} . s^{-1} was obtained and taken for I_{max}.

K_m, the Michaelis constant, and

C_{lmin}, the minimum concentration at the root surface, were determined in an uptake experiment with nutrient solution by the method of Claassen and Barber[3]

r_0, root radius was measured with a microscope from roots of the pot experiment mentioned above.

L, root length, was obtained with the method of Newman[10] from the root systems of the same pot experiment after the soil had been washed off the roots.

θ, volumetric water content, was determined by weight with bulk density taken into account.

D_e, effective diffusion coefficient, was determined according to the method of Vaidyanathan and Nye[17]. Missing values were found by interpolation from Fig. 2 in Kuchenbuch *et al.*[9]

v_0, water flux through the soil surface, was assumed to be $5 \cdot 10^{-8}$ cm $\cdot$ s^{-1} according to experience. (According to the experimental design water flux was relatively low).

b, potassium buffer power: $\Delta C/\Delta C_1$ at the beginning of the experiment. This value was assumed to be constant over the period of the experiment.

ΔC, diffusible potassium, was taken from the maximum depletion of exchangeable potassium at the root surface by using the method of Kuchenbuch and Jungk[8].

C_{li}, initial K concentration of the soil solution, was determined from displacement of the soil solution according to Adams[1]

r_1, mean half distance between roots.

Procedure for calculating K uptake

The change of K concentration of the soil solution in the vicinity of roots was calculated for the first period of 19 days. The data were taken from Table 1 for a pot with $\theta = 0.26$, except C_{li} was 1.1 μmol/ml. After this initial period with equal water content in all pots, soil solution was decreased to 0.75 μmol K/cm^3. For the second period of 19 days, the parameters of Table 1 were used to calculate K uptake for pots of different water content. In this case the assumption was made that the root uptake parameters – I_{max}, K_m, C_{lmin} – did not change with root age.

Procedure for calculating the influence of soil texture on the availability of K

In order to determine the effect of soil texture on the availability of K, two different soils were used: the plough layers of

- a loess derived silt loam, 12% clay, 1.8% organic matter
- a sandy soil, 2% clay, 3.3% organic matter

The relation beween water content and water tension was determined with the suction method as described by Hartge[7] (p.72). The plant parameters I_{max}, K_m, r_0, r_1 and v_0 as well as the soil parameters C_{li}, C, and b were taken from the pot experiment described above, from the treatment $\theta = 0.09$. The effective diffusion coefficient was calculated according to

$$D_e = D_l \theta f \frac{1}{b}$$

D_l is the diffusion coefficient of K in water: 1.98×10^{-5} $cm^2 \times s^{-1}$.

Table 1. Plant and soil parameters for simulating K uptake of onion roots grown in Söderhof silt loam at different volumetric water content

θ, cm^3 cm^{-3}	D_e, cm^2 s^{-1} 10^{-7}	r_1, cm	RD, cm cm^{-3}
0.07	0.8	0.32	3.11
0.08	0.8	0.41	1.87
0.09	0.8	0.32	3.01
0.11	1.0	0.28	3.95
0.17	2.4	0.30	3.51
0.18	2.4	0.27	4.27
0.19	2.4	0.22	6.52
0.26	4.2	0.27	4.27
0.36	7.5	0.30	3.42
0.36	7.5	0.27	4.27
0.37	7.5	0.33	2.94
0.42	11.2	0.25	5.05
0.43	11.2	0.23	5.81

Tabelle 1. Boden- und Pflanzenparameter zur Berechnung der K-Aufnahme von Zwiebelwurzeln bei unterschiedlichem Wassergehalt eines Lössbodens (Boden Söderhof)

Parameters which were the same for all treatments:

$I_{max} = 2.9$ μmol $cm^{-2} s^{-1}$; $K_m = 0.02$ μmol cm^{-1}; $C_{lmin} = 0.002$ μmol cm^{-3}; $r_0 = 0.027$ cm; $v_0 = 5 \times 10^{-8} cm^{-3} cm^{-2} s^{-1}$; $C_{li} = 0.75$ μmol cm^{-3}; b = 3.42; time of uptake = 19 days

– Water content θ was read off the pF, matric potential, curve for respective water tensions, and

the impedance factor, f, derived from the relation between θ and f as published by Rowell *et al.*[14].

Results

The parameters used for the model calculation of the pot experiment are summarized in Table 1. As can be seen, the effective diffusion coefficient increased by a factor of about 10 as the volumetric water content increased from 0.1 to 0.4. Root density RD, which is given by

$$RD = \frac{1}{\pi r_1{}^2}$$

also tends to increase with water content.

In Figure 1 measured potassium uptake of the onion plants is compared to uptake calculated with the model. As can be seen, K uptake increases with increasing water content of the soil. The line drawn into the diagram indicates complete agreement between calculated and measured uptake. The agreement of the calculation is good in the range of θ = 0.17 to 0.37; however, the model somewhat underestimates K uptake at high soil moisture and overestimates uptake at low soil moisture. Nevertheless, the results indicate, that the calculated values

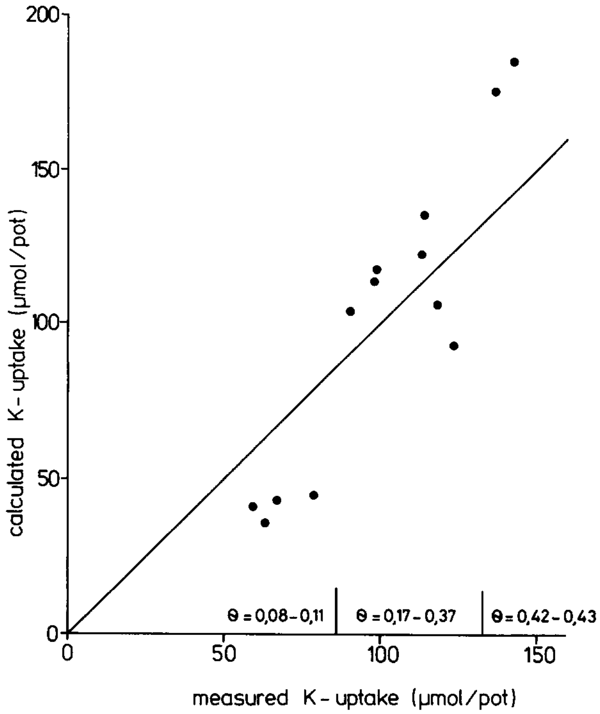

Fig. 1. Comparison of measured and calculated potassium uptake of onion plants at different moisture levels of the soil (soil: Söderhof silt loam, potassium uptake between 19 and 38 days after transplanting).

Abb. 1. Vergleich der berechneten und gemessenen Kalium-Entzüge durch Zwiebelpflanzen bei Variation des Wassergehaltes (Boden Söderhof; Kaliumaufnahme zwischen 19 und 38 Tagen nach Pflanzung).

do not markedly deviate from reality. The model therefore appears to be useful for investigating the reasons which caused the variation in K uptake.

Of main interest is the change with time of the potassium distribution around the root over the distance of r_1. In Figure 2 an example is given for $\theta = 0.09$. Under these relatively dry conditions, the K concentration at the root surface is strongly reduced compared to more distant parts of the soil (Fig. 2a). From this pattern of depletion, the rate of K uptake per unit of root surface is reduced to about half within 7 days (Fig. 2b). However, under the root density observed in the pot experiment, the K concentration between adjacent roots was also reduced to about one third of the initial value, within the period of 19 days. In Fig. 2c and 2d, an example is given for a relatively high water content of the soil. Compared to the dry soil the gradients of the K concentration in the rhizosphere are much less.

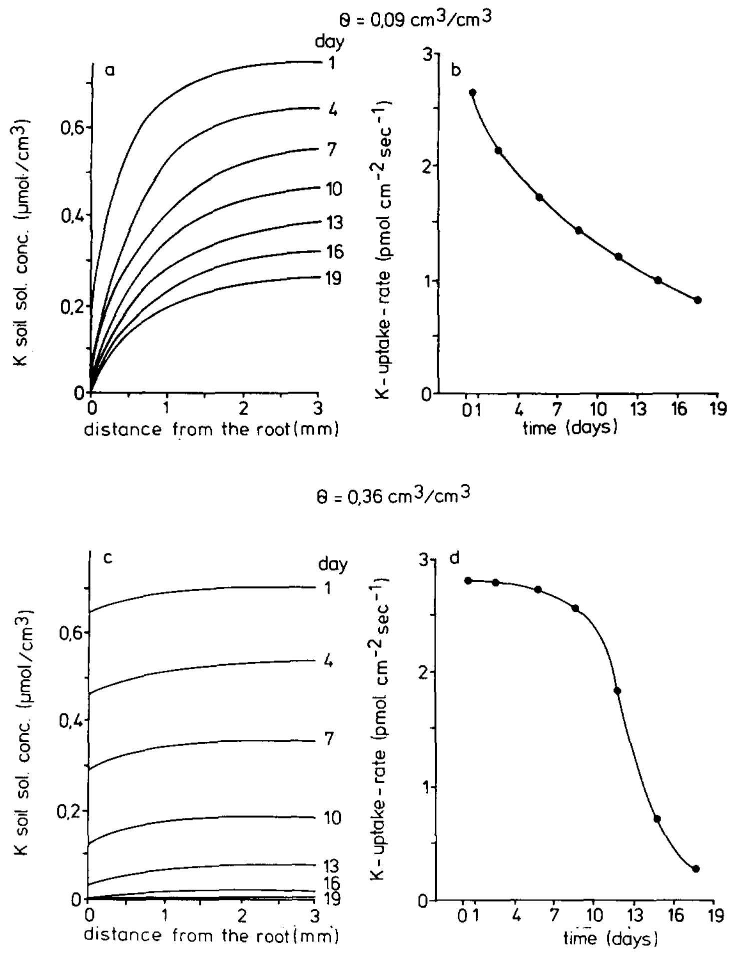

Fig. 2. Potassium depletion in the vicinity of onion roots and K uptake rate as a function of time of uptake at two moisture levels of the soil (Söderhof silt loam).
Abb. 2. Einfluss der Zeitdauer und des Wassergehaltes des Bodens auf die K-Verarmung des wurzelnahen Bodens sowie K-Aufnahmerate von Zwiebelwurzeln (Boden Söderhof).

On the other hand, K concentration in the soil between two roots decreased faster. The rate of depletion of the total volume of soil was almost equal within the first 13 days of the experiment and slowed down afterwards; after 19 days the soil was almost devoid of K.

Potassium uptake rate of the roots was almost constant during the first 10 days (Fig. 2d). This occurred because roots were absorbing K at almost maximum rate and K transport to the root was not limiting. Soil solution K at that time was reduced to 0.1 μmol ml^{-1}. From this point, the rate of K uptake decreased rapidly.

Table 2. Influence of reduced root growth on K uptake of onion plants due to low soil water content

	θ = 0.09	θ = 0.36
Observed root length, cm	193	276
Calculated K uptake, μmoles/pot	67	118
Assumed root length, cm	276	–
Calculated K uptake, μmoles/pot	89	

Tabelle 2. Einfluss des geringeren Wurzelwachstums durch niedrigen Wassergehalt des Bodens auf die K-Aufnahme von Zwiebelpflanzen

Table 3. Influence of soil matric water potential on the parameters of K mobility in two soils

Matric potential pF	Soil texture	θ, cm^3 cm^{-3}	f	D_e, 10^{-8} cm^2 s^{-1}
2.0	sand	0.23	0.17	15.7
	loam	0.42	0.52	89.0
2.5	sand	0.16	0.06	3.5
	loam	0.36	0.42	60.5
3.0	sand	0.12	0.04	1.7
	loam	0.30	0.31	37.0
3.7	sand	0.10	0.02	0.8
	loam	0.19	0.12	9.4
4.2	sand	0.08	0.02	0.7
	loam	0.13	0.04	1.8

Tabelle 3. Einfluss des Matrixpotentials des Bodenwassers auf die Mobilitätsparameter von K in zwei Böden

Parameters which were used for all treatments:
C_{li} = 0.75 μmoles cm^{-3}
ΔC = 3.64 μmoles cm^{-3}
b = 4.85

Total uptake of K at moisture levels of 0.09 and 0.36 was calculated to be 67 and 118 μmol K per pot, respectively (Table 2). The difference is due to both rate of K uptake per unit of root and root growth. If root length of the high moisture level is used to calculate K uptake at θ = 0.09, a value of 89 μmol K per pot is obtained. This means 43% of the difference in K uptake between the moist and the dry soil is due to root growth.

So far, only the relation between water content and availability of K was regarded. However, plant growth presumably depends on water

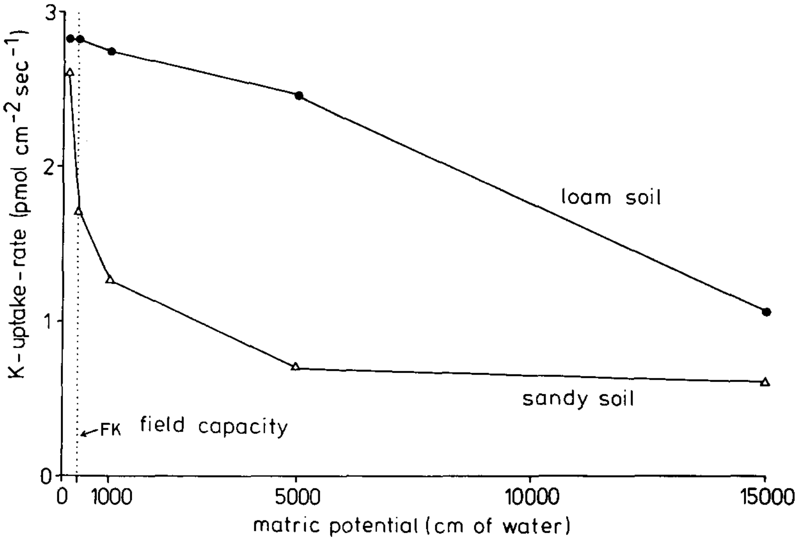

Fig. 3. Average K uptake rates of onion roots in a loam and a sandy soil calculated by the simulation model as a function of matric potential. (Time of uptake: 19 days)
Abb. 3. Vom Simulationsmodell errechnete mittlere K-Aufnahmerate für einen Löss- bzw. Sandboden in Abhängigkeit von der Wasserspannung. (Dauer der Aufnahme: 19 Tage).

tension of the soil if nutrients are not limiting. Table 3 shows the water content of specific values of water tension for a loess and a sandy soil. Both soils have similar total pore spaces. However, above pF 2, water content decreases in the sandy soil much faster than in the loess soil. Therefore, in the range of the available water (pF 2.5 to 4.2), the parameters of potassium mobility – θ, f and D_e – are markedly lower in the sandy compared to the loam soil. At pF 3, the diffusion coefficient in the loess soil is about 20 times higher than in the sandy soil. This can be considered the reason for the big differences in the rate of K uptake of onion roots. As shown in Fig. 3, the rate of K uptake from the sandy soil decreased drastically between saturation and 1000 cm of tension (pF 3), whereas in the loess, K uptake rate stayed almost at its maximum level until 5000 cm of tension (pF 3.7). One half of I_{max} was reached between pF 2.5 and 3 in the sandy soil, but beyond pF 3.7 in the loess soil.

In order to demonstrate the effect of soil texture on K distribution around the root and rate of K uptake of the roots, results of calculations at pF 3 are shown in Fig. 4. As can be seen, the decrease of K concentration at the root surface is much stronger in the sandy soil compared to the loess soil. On the other hand, change of concentration in the soil between adjacent roots was much less in the sandy

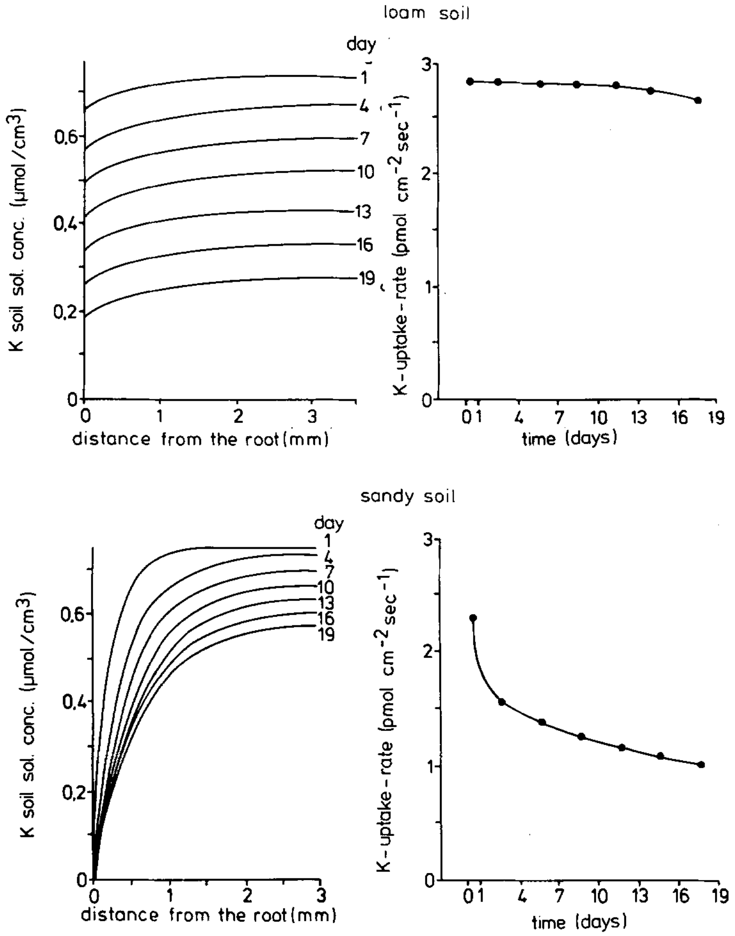

Fig. 4. Potassium depletion in the vicinity of onion roots and K uptake rate as a function of time and uptake in a loam and a sandy soil at a water potential of pF 3.
Abb. 4. Konzentrationsabsenkung und K-Aufnahmerate von Zwiebelwurzeln in Abhängigkeit von der Aufnahmedauer in einem Löss- und einem Sandboden bei einer Wasserspannung von pF 3.

soil. As a result of the depletion at the root surface, rate of K uptake remained almost unaffected in the loess over the period of 19 days, whereas in the sandy soil, K uptake rate fell below 50% of the maximum wihtin 4 days. From these data, a K uptake of 0.95 μmol from the sandy soil and 2.5 μmol from the loess soil was calculated.

Discussion

The comparison of measured and calculated K uptake of onion plants (Fig. 1) showed that the mathematical model, based on soil and plant parameters predicts K uptake fairly well.

The deviations observed at very low and high water contents may be attributed to differences in root growth. In the calculation constant root growth was assumed for all water contents. However, as found in part 1 for low value of θ this may not be a valid assumption. From the result in Fig. 1, it may therefore be concluded that the conception of the model is essentially realistic and that the parameters used are fairly right. Under this assumption the model can be used to calculate relationships in the soil-plant system which cannot be measured. This is the case with the distribution of K in the soil around single roots and their K uptake rate over time.

The calculations show that the soil water content has a strong influence on the shape of the depletion profile. Low water content resulted in narrow zones of depletion with steep gradients. With the root density found in this experiment, only part of the soil volume contributed K to the plant. On the other hand, with high water content in the soil the gradients are not as steep so that the whole volume of soil is almost equally depleted from K. Therefore, drying of a soil reduces the volume of the soil that feeds the plant and speeds up K depletion at the root surface which finally limits the rate of K uptake per unit of root. The same soil maintained at a higher moisture level enables the root to sustain high rates of K uptake over much longer periods of time.

Therefore, at the same K content of the soil, K uptake per unit of root strongly depends on the water content of the soil because of its influence of K mobility. However, root growth may also be reduced by low water content of the soil, as has been shown in the first part of the work. This may be an additional factor of potassium availability.

Potassium mobility depends on the volumetric water content (θ) but plant growth depends on the water tension of a soil. At pF 2, the two soils in this experiment were similar in their K supplying power (which can be attributed to both water content and tortuosity). Because the soils are different in their water content – water tension relationship (Table 3), differences in K transport at higher pF values should be expected – the loess should be superior to the sandy soil. The conclusion from Figure 4 is that the K supplying power of the sandy soil is much more sensitive to changes in water tension than the loess. The advantage of the simulation model is that the degree of this effect can be shown. The model thus provides information on processes of the soil-plant system which cannot be measured directly with individual roots.

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