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Roots regulate ion transport in the rhizosphere to counteract reduced mobility in dry soil

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Abstract

Diffusion of ions in the soil depends on soil moisture content. In a dry soil, transport of nutrients towards the root and the concomitant uptake could be reduced. However, pot and field experiments showed that this is not always the case. The objective of this paper was to investigate possible mechanisms of plants to counteract reduced nutrient supply due to water shortage. A split root system was used to investigate P and K inflow of oat and sugar beet at different soil moisture contents (Θ) without water shortage for the plant. The measured average P and K inflows were compared to model calculations considering diffusion, mass-flow, sorption and uptake processes. In the calculations, soil dryness impeded diffusion and decreased nutrient inflow as expected. Measured K inflow was decreased in a similar way indicating that Θ influences K diffusion. In contrast to this, measured P inflow was not influenced by Θ and under-estimated by the model. Low and high molecular exudates were collected at different water supply levels showing that exudation rate of both compounds was increased at water shortage. Especially the high molecular exudates (i.e. mainly mucilage) from water-stressed plants increased P concentration in soil solution under dry conditions in an incubation experiment. Calculated inflow considering this increased P concentration agreed well with measured P inflow indicating that exudation of mucilage could be a mechanism to overcome nutrient transport problems due to soil dryness.

Introduction

A low soil moisture content may reduce nutrient uptake. This could be due to (I) a reduced nutrient demand of the plant because of an impeded plant growth at water deficiency, (II) a smaller root system at water shortage (Mackay and Barber, 1985a) and (III) impaired diffusive conditions, which decrease transport of nutrients towards the root and concomitantly inflow into the root (Kuchenbuch et al., 1986).

In contrast to these theoretical considerations, Schmid and Claassen (1994) found no relation between soil water content and P inflow of sugar beet grown in the field. This confirms frequent observations that a dry topsoil does not reduce plant growth and uptake of P and K as long as the plant is able to take up sufficient water or nutrients from the subsoil. However, even in pot experiments without a supply from subsoil P and K inflow of maize was not influenced by soil water content (Mackay and Barber, 1985a, b). This points to the ability of plants to increase nutrient availability under dry conditions.

The objective of this paper was to investigate mechanisms that enable plants to maintain a high P and K inflow despite adverse diffusive conditions due to soil dryness. In contrast to other papers (e.g. Dunham and Nye, 1976), emphasis was laid on a good water and nutrient supply, so that soil dryness only affected soil transport of P or K.

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Material and methods

Pot experiment

Oat and sugar beet were grown under controlled conditions (16/8 h day/night; 22 °C/18 °C, 50% relative humidity, 260–300 μE m^{-2} s^{-1}). A special pot design was used (Figure 1) to avoid water stress despite dry soil conditions (Seiffert et al., 1995). The upper part of the pot was filled with 2 kg soil, the bottom part with nutrient solution. There was no contact between soil and solution. For the P experiment, subsoil from a luvisol was used (20% clay, 75% silt, 5% sand, 1.3 g cm^{-3} density) containing 27 mg P kg^{-1} soil as determined by the calcium-acetate-lactate (CAL) extraction method (Schüller, 1969), which is classified as a low supply level by the German fertilizer recommendation scheme. The P concentration in soil solution was 1.7 μM. For the K experiment, a fluvisol was used (33% clay, 31% silt, 36% sand, 1.5 g cm^{-3} density), which had a high K fixing capacity, where hardly any plant growth is possible. The soil was fertilized with 5 and 10 mmol K kg^{-1}. In both experiments, the soil was fertilized with 100 mg N kg^{-1} as $Ca(NO_3)_2$ and covered by a sand layer to reduce evaporation. In the P experiment, the volumetric soil water contents (Θ) were adjusted to 0.13, 0.16, 0.19 and 0.26 for oat. Because it was difficult to adjust differences of Θ in steps of 0.03 (from 0.13 to 0.19) only 3 moisture treatments (0.13, 0.17 and 0.24) were chosen for sugar beet. In the K experiment, Θ was set to 0.18, 0.26 and 0.30 for both species. In both soils, the highest Θ was close to field capacity. To ensure a homogeneous water distribution, the water was added through a hose system connected to synthetic fibre wicks, which wound through the soil. To keep Θ constant at the desired levels, water was added at least daily according to pot weight. Soil water content was measured after the last harvest. This ensures that the growth of the young plants did not add a considerable mistake to the adjustment of soil water by weight.

The soil filled in the upper part of the pots was divided from the bottom part by a net that allowed roots to grow through. The bottom part was filled with aerated nutrient solution (1 mM $Ca(NO_3)_2$, 0.1 mM $MgSO_4$, 18 μM Fe as Fe-EDTA, 45 μM H_3BO_4, 14 μM $MnCl_2$, 0.8 μM $ZnSO_4$, 0.3 μM $CuSO_4$, 1 mM KCl or 1 mM NaH_2PO_4), lacking the nutrient under examination (P or K). Thus, plants could get all nutrients and water from the solution with the exception of P or K, which could only be taken up from the soil at different moisture contents.

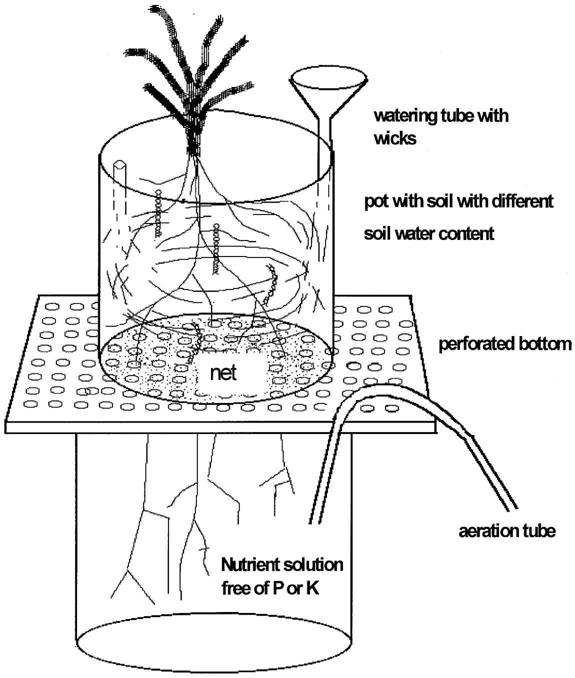

Figure 1. Design of the split-root pots.

A first harvest took place 14 days after sowing (DAS) in the P experiment and 17 DAS in the K experiment. Up to the first harvest all plants grew at a Θ of 0.24. The differentiation in soil water by irrigation or withholding water started immediately at the day of the first harvest. It took 3 days at longest until the desired water content was adjusted. The second harvest was at 24 DAS (P) and 27 DAS (K). At each harvest, shoot dry matter was weighed and the P or K concentration herein was determined colorimetrically (Kitson and Mellon, 1944) or by flame photometry, respectively, after wet digestion with a mixture of HNO_3, $HClO_4$ and H_2SO_4. Root length was measured by a line intersection method (Tennant, 1975) separately for roots grown in soil and solution. Root radius was measured under a microscope. For determining root hair length and density, roots were cut into 1 cm pieces and about 100 of them were sorted by eye into three classes according to their root hair density. From each class about 20 root pieces were taken to count number of root hairs per cm root cylinder and determine total root hair length with an intersection method under the microscope (Brewster et al., 1976). Root hairs were only measured at soil grown roots at the second harvest in the P experiment, the data were also taken for modelling the K experiment. Average P or K inflow was calculated according to Williams (1948) by the amount of nutrients taken up between the two harvests and an exponential root length development in the soil. There were four replicates per treatment.

Model calculations

Measured inflow was compared to a calculated one. Calculations were performed with the transport and uptake model (NST 3) of Claassen et al. (1986). This model calculates soil transport of nutrients by diffusion and mass-flow, taking sorption processes into account, and uptake by the Michaelis-Menten kinetics. The necessary input parameters were derived as follows: the diffusion coefficient in water (D_L) was taken form Edwards and Huffman (1959) and Parsons (1959) for P (8.9×10^{-6} cm^2 s^{-1}) and K (19.8×10^{-6} cm^2 s^{-1}), respectively. The volumetric soil water content (Θ) was taken according to the treatments. The model calculates with a constant Θ during the whole calculation period. Changes or spatial distribution due to water uptake and irrigation could not be taken into account. The impedance factor (f) was calculated from Θ according to Bhadoria et al. (1991). Under the assumption that the sand layer on the soil impeded evaporation the reduction in soil water content was solely due to plant uptake. Hence, the water-flow in the soil towards the root could be calculated by the amount of irrigation water which was used to keep Θ constant, average root length, and time period between the harvests. Soil solution was derived in a displacement procedure according to Adams et al. (1980) after the harvests and P or K concentration herein was determined colorimetrically (Murphy and Riley, 1962) or by flame photometer, respectively. Buffer power (b) was calculated from the CAL extractable P or NH_4Oac-exchangeable K and the soil solution concentrations. Both were measured for each treatment at the second harvest. Buffer power was taken as linear because the consideration of the non-linearity of buffer power has little influence on transport calculations (Steingrobe et al., 2000). Because the used soils were poor in P or K it was more likely that transport conditions in the soils played a much more important role for nutrient acquisition than the uptake kinetics (Claassen and Steingrobe, 1999). Therefore, parameters of the Michaelis-Menten kinetics were taken from literature (Jungk et al. 1990; Meyer and Jungk, 1993). The importance of the Michaelis-Menten and other parameters for the calculation results was derived in sensitivity analyses where each parameter was changed by a factor of 0.1 to 10.

Root exudates

To investigate the influence of water supply on exudation patterns, cold and warm-water soluble exudates were collected. Oat was grown in sand with 15 plants per 3 L-pots at sufficient water supply. The sand was fertilized per kg with: 160 mg N, 250 mg K, 30 mg Mg and 6 mg P and micronutrients. After 10 days, water contents were adjusted to 30, 50 and 70% water capacity, which took 3 days. After another 19 days, the plants were washed out of the sand very carefully to minimize root injuries. Afterwards the roots were transferred into a washing solution (0.05 mM $CaCl_2$) for 1 h so that injured root cells could bleed out. The $CaCl_2$ solution was renewed and roots could release exudates into the fresh solution for 2 h at room temperature (cold-water soluble exudates, CSE). Afterwards, the plants were transferred to a $CaCl_2$ solution at 60 °C for 5 min to collect warm-water soluble exudates (WSE). Both solutions were freeze-dried to concentrate CSE and WSE. Root length was determined by a line intersection method according to Tennant (1975) to calculate exudation rates. There were 6 replicates per treatment.

To investigate the influence of the root exudates on P and K availability, the luvisol subsoil was incubated with the CSE and WSE. Seven days before incubation antibiotics (250 ppm streptomycin and 25 ppm novobiocin) were added to the soil to reduce microbial activity. The concentration of WSE and CSE in the rhizosphere were not known and data in literature vary in a wide range (Jones, 1998). Therefore, the concentrations of CSE and WSE chosen for the incubation experiment were calculated based on several assumptions. The concentration gradient of carboxylic acids can range 0.2 to 1 mm from the rhizoplane into the soil (Jones, 1998). Accordingly, we assumed that the CSE are exuded in the soil 0.5 mm around the root, which is also in the size of P depletion. For a root radius of 0.12 mm, this is a soil volume of 0.011 cm^3 or, at a soil density of 1.3 g cm^{-3}, a soil weight of 0.015 g around 1 cm of root. During the exudation period of two hours the plants exuded around 1.4 μg CSE cm^{-1} root. This means roughly a concentration of 0.1 mg CSE g^{-1} soil. For WSE, which adhere to the root, the assumed rhizosphere thickness was 0.2 mm. This was in the order of measured root hair length. This resulted in a concentration of 1 mg WSE g^{-1} soil.

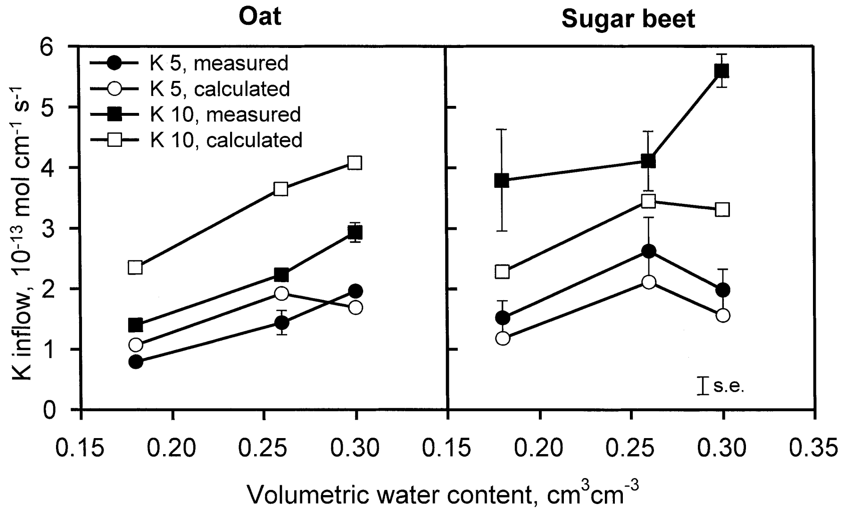

Figure 2. Influence of volumetric water content on measured and calculated K inflow of oat and sugar beet in a fluvisol at two fertilizer levels (K5: 5 mmol K kg^{-1} soil; K10: 10 mmol kg^{-1}).

After mixing the exudates of each water supply level in 1 kg of soil, the soil was watered to volumetric water contents of 0.16 and 0.28. Furthermore, controls without any exudate and with a mineral fertilization according to the mineral P and K content of the exudates (0.5–0.6 mg and 60–100 mg g^{-1} exudate, respectively) were prepared accordingly. After 5 days of incubation at 4 °C, soil solution was collected by a displacement method (Adams et al., 1980) and P and K concentration herein was determined as described above. The incubation was not replicated, but soil solution was taken in four parallels.

Results and discussion

Influence of soil moisture content on K inflow

In the K experiment, yield level was lower than in the P experiment (Table 1). Due to the high K fixation capacity of the soil plants suffered from K shortage even at the high K supply level. In the K 10 treatment, plant growth and K concentration in plant dry matter of oat was decreased by low soil water content. At the low supply level, yield reduction due to soil dryness was not stastically significant, although K concentration in oat was also reduced. Root length was less affected (not shown), hence, the reduced K uptake was rather due to a low K inflow (Figure 2). For oat, an increase of Θ from 0.18 to 0.30 doubled measured average inflow in both fertilizer treatments. For sugar beet, this increase was less pronounced, which was mainly due to a lower K concentration in soil solution. Furthermore, a high soil water content (Θ) reduced root hair length and density of sugar beet in the P experiment (not shown) which might also be given for the K experiment in which root hairs were not measured. The impeded root hair growth reduced total root surface area per unit root cylinder length, which concomitantly reduced inflow related to root cylinder length. Calculated and measured inflow agreed well at the lower K supply, however, differences occurred in the high K treatments. For oat, the model over-estimated K inflow, whereas for sugar beet, calculated values were too low.

A sensitivity analysis was performed where the input parameters of the model were changed in the range of 0.1 to 10 times the initial value to show possible reasons for the differences between measured and calculated inflow. It revealed that the uptake parameters (I_{max}, K_m and C_{Lmin}) as well as the buffer power had no or only a limited influence on calculated inflow, whereas the relation between the initial soil solution concentration (C_{Li}) and inflow was nearly linear. This is typical for situations where nutrient transport in the soil limits uptake. El Dessougi and Claassen (2003) presented similar results of a sensitivity analysis on a K fixing soil. Furthermore, the over-estimation in the K 10 treatment of oat disappeared in the sensitivity analysis by ‘switching off’ the root hairs. Root hair length was only measured in the P experiment and also used for calculating K uptake. It is known that P deficiency increases root hair growth (Foehse and

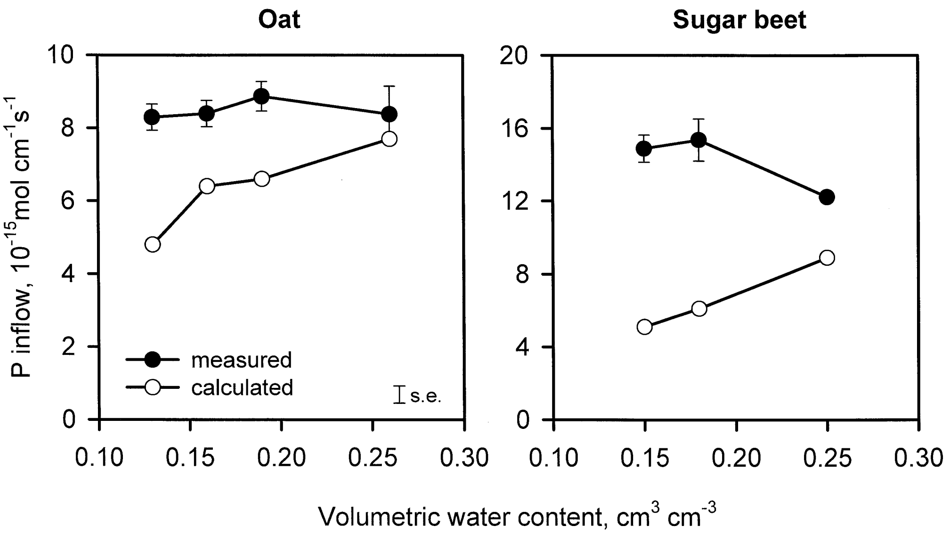

Figure 3. Influence of volumetric water content on measured and calculated P inflow of oat and sugar beet grown in a luvisol subsoil.

Jungk, 1983), therefore, it is possible that root hairs in the K experiment were less than assumed in the calculations. The under-estimation for sugar beet could only be 'corrected' in the sensitivity analysis by increasing C_{Li}, which points to the fact, that sugar beet is able to increase K availability in a way that is not described by the model.

Of more interest for this study is, however, that the slope of calculated and measured inflows is similar, especially for oat. Hence, the influence of Θ on measured soil transport and inflow of K was as described by the model. It seems, that neither oat nor sugar beet were able to counteract the negative influence of soil dryness on K diffusion.

Influence of soil moisture content on P inflow

In contrast to K, low Θ had no influence on yield of both species in the P experiment and reduced only for oat the P concentration in dry matter (Table 1). The measured inflow was independent of Θ (Figure 3). Calculated inflow in both species, however, was much less than the measured inflow and was strongly influenced by soil water content. This indicates that plants were able to increase P availability in a way that is not described by a sorption, diffusion and mass-flow model. The sensitivity analysis revealed that only an increase in C_{Li} could have such an effect, like it was also shown by Bhadoria et al. (2002). More interesting for this study, however, was that both plant species were able to overcome the negative effect of soil dryness on P transport in the soil.

There are several possible processes for plants to increase P availability and uptake like an altered root and/or root hair morphology, mycorrhiza or chemical changes in the rhizosphere. Root and root hair morphology was considered in the calculations. Mycorrhiza does not develop on sugar beet. The oat plants were very young, therefore we hypothesize that mycorrhiza was hardly established and played no major role in P acquisition. Thus, in this study we were interested in which way soil dryness alters the amount and/or quality of exudates as collected in cold and warm water.

Cold-water and warm-water soluble exudates

Oat was grown in sand at 30, 50 and 70% water capacity, where 70% corresponded to about 13% volumetric water content. Shoot dry matter after at all 32 days of growth was 310, 380 and 480 mg plant^{-1}, respectively, showing the water stress in the dry treatments. The water content of the sand had also a strong influence on the release of both cold-water soluble exudates (CSE) and warm-water soluble exudates (WSE) of oat (Figure 4). At 30% water capacity exudation of CSE and WSE was more than doubled compared to moist conditions at 70% water capacity. Total exudation (CSE + WSE) was between 2.5 and 6.3 μg cm^{-1} root which is about 7–15% of root dry weight. This is in accordance to Campbell and Greaves (1990), who reported of 3–15% of root weight for mucilage, soluble exudates and root cap. They pointed also to large differences that may occur to comparable studies be-

Table 1. Influence of the volumetric soil water content (Θ) on dry matter yield and P or K concentration in dry matter of oat and sugar beet (different letters asign significant differences, Tukey $P < 0.05$)

		P experiment		K experiment			
				5 mmol K kg^{-1} soil		10 mmol K kg^{-1} soil	
	Θ	shoot dry matter	P conc. in dry matter	shoot dry matter	K conc. in dry matter	shoot dry matter	K conc. in dry matter
	cm^3 cm^{-3}	mg plant^{-1}	mg g^{-1}	mg plant^{-1}	mg g^{-1}	mg plant^{-1}	mg g^{-1}
Oat							
	0.13	544 a	1.4 a				
	0.16	542 a	1.8 b				
	0.19	574 a	2.0 c				
	0.26	523 a	2.1 c				
	0.18			150 a	24 a	160 a	32 a
	0.26			170 a	30 b	210 ab	38 b
	0.30			170 a	35 c	220 b	43 b
Sugar beet							
	0.13	938 a	2.5 a				
	0.17	870 a	2.9 a				
	0.24	1017 a	2.4 a				
	0.18			100 a	16 a	130 a	31 a
	0.26			160 b	20 a	180 ab	35 a
	0.30			100 a	20 a	240 b	33 a

cause measured rhizodepositons depends much on the physiological state of the plants and of course depends on the methods to collect the exudates. An increase of exudates under dry conditions was also found by Czarnes et al. (2000) for maize.

These exudates were added to a luvisol subsoil to determine their ability to increase P and K availability in the soil. Phosphate concentration in soil solution was slightly increased after adding CSE to the soil in a concentration derived by the exudation in 2 h and a distance of diffusion 0.5 mm around the root (Figure 5). There was no difference between the exudates from plants grown at different water supplies. Cold-water soluble exudates contain mainly amino acids, sugars, and organic acids. It is known that organic acids, especially citrate, are able to increase P availability by complexing possible metals responsible for strong interactions with P, by ligand exchange (Gerke, 1992), or by binding phosphate in an iron-phosphate-citrate complex that facilitates transport towards the root (Gardner et al., 1983). However, the relevance of these processes is uncertain (Hinsinger, 2001), because a measurable increase of P availabilty is only given at very high concentrations of organic acids in the soil. In a luvisol comparable to ours, an effect of

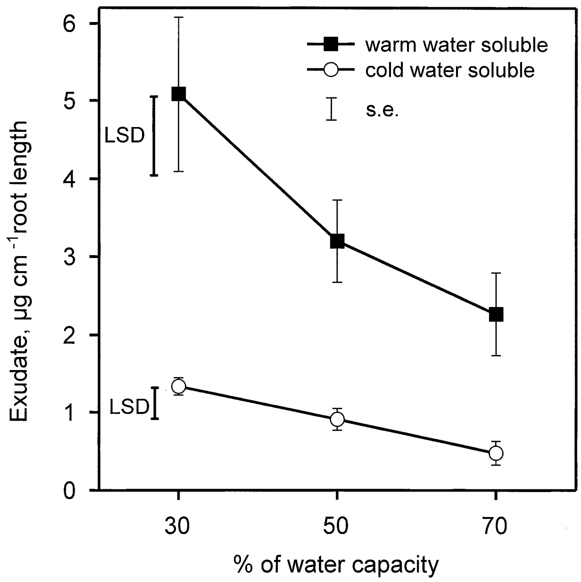

Figure 4. Influence of water supply in sand culture of oat on the exudation of cold (CSE) and warm (WSE) water soluble exudates. (LSD from Tukey-test at $P = 0.05$).

citrate on P availability was found at concentrations of 20 μmol g^{-1} (Gerke, 1992) and Beißner (1997) reported a significant increase of P in soil solution

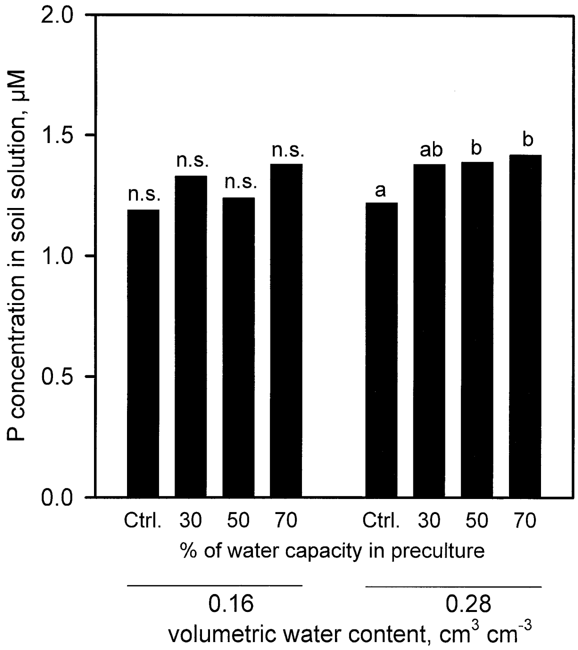

Figure 5. Influence of cold-water soluble exudates (CSE) that were collected from plants grown at different water supply on P concentration in soil solution in an incubation experiment at volumetric water contents of 0.16 and 0.28. (n.s. no significant differences; different letters asign significant differences, Tukey $P < 0.05$).

at additions from 60 μmol caboxylic acids g^{-1} soil onwards. Compared to this we had very low concentrations, which might be the reason for the low effect of CSE on P availability. Assuming that all 0.1 mg exudates would be citrate, this would amount around 0.5 μmol g^{-1} soil. Furthermore, a possible beneficial effect of microorganisms on the P availability in the rhizosphere was unlikely in the incubation experiment because microorganism activity was reduced by antibiotics and low temperatures.

Adding CSE to the soil did not increase availability of K (not shown). The slight increase in K soil solution concentration that could be measured was solely due to a fertilizer effect of the high K concentration in the exudates.

Warm-water soluble exudates, which are assumed as being mainly mucigel substances, contained also K and small amounts of P. To distinguish between the influence of the exudates on P and K availability and a simple fertilization effect by the exudates, mineral P and K was fertilized in an amount comparable to that supplied with the exudates in a further experiment. The untreated controls in the incubation and fertilization experiments gave slightly different values in the measured P soil solution concentration. Therefore, the comparison between fertilizer effect and release of P by WSE was done on a relative scale (Figure 6). The mineral fertilization increased P soil solution concentration by about 20% independent of soil moisture as shown in Figure 6a. This is relatively high, as the applied amount of P (0.04 μmol g^{-1} soil) should have increased P solution concentration by only 5% when the buffer power of 611 is taken into account. Adding WSE to the dry soil ($\Theta = 0.16$) increased P concentration by about 50%. Thus, WSE positively influenced P availability. However, there were qualitative differences between exudates from plants grown at water shortage and well-watered plants. The effect of WSE from plants grown at 70% water capacity was equal to the 'fertilizer' effect. Furthermore, the positive effect of the exudates was only observed in the dry soil. At a volumetric water content of 0.28, the exudates even lowered the P concentration in soil solution.

The positive effect of mucilage on the P concentration in soil solution can be caused by the carboxyl groups of e.g. polygalacturonate (PGA) which is a major component of the mucilage. Phosphate that is bound to Fe-/Al-oxides and hydroxides can be exchanged by carboxyl groups as it was shown by Gerke et al. (2000) for carboxylates, who found a relationship between sorption of carboxylate anions to the soil matrix and the release of phosphate into soil solution. Nagarajah et al. (1970) reported that polygalacturonate lowers the adsorption of phosphate to goethite or gibbsite, which might also be due to an exchange process. Furthermore, the long chains of polygalacturonate may cover soil particles, which stabilizes the particles (Morel et al., 1991) and reduces the possibility of re-adsorption of phosphate (Grimal et al., 2001). Grimal et al (2001) showed that the sorption of P to goethite was less in presence of pure PGA compared to mucilage which was derived from field grown maize. Differences in the P releasing effect of the different WSE could, therefore, be due to different concentrations of PGA. Polygalacturonate is also able to bind large amounts of water, which facilitates soil penetration by roots under dry conditions. Hence, it might be speculated that the PGA concentration in the mucilage is increased at soil dryness. Like it is shown for the moist soil in Figure 6, Grimal et al. (2001) found also a decrease of P in solution due to mucilage, when the mucilage was added after P was adsorbed to the goethite. They did not provide any explanation for this observation, but perhaps might the covering of

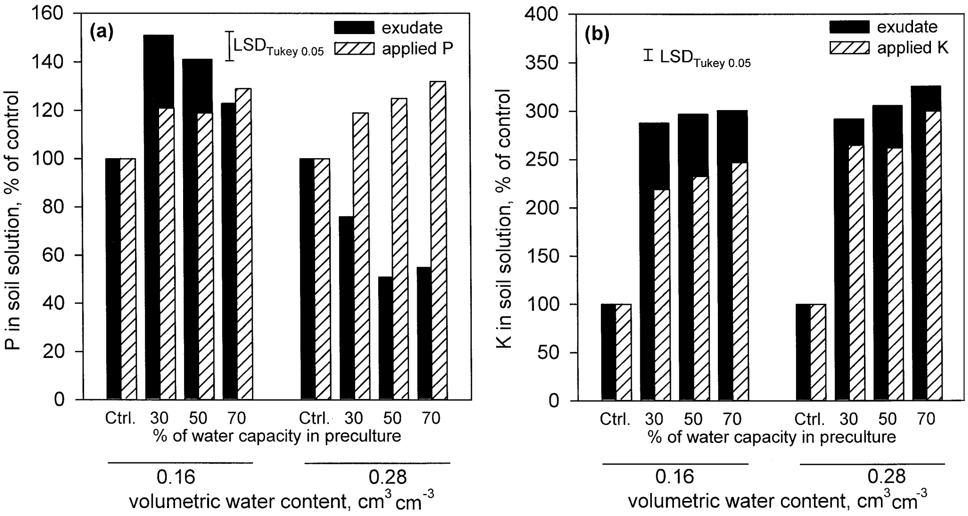

Figure 6. Influence of warm-water soluble exudates and a mineral fertilization according to their P and K content on the (a) P and (b) K concentration in soil solution at volumetric water contents of 0.16 and 0.28. The concentrations are shown relative to a control without added exudates or mineral P and K. The plants were grown at different water supply before taking the exudates.

soil particles by mucilage may also hinder exchange processes with sorbed P.

For K, most of the effect of WSE on K concentration in soil solution was caused by the K content of the exudates (Figure 6b). However, there was a small K releasing effect caused by the organic compounds of the exudates. Due to its high content of carboxyl groups mucilage is able to bind and exchange cations, especially protons and Ca ions. Exchange with potassium that is sorbed to clay minerals may thereby take place, which might increase the availability of K. Like for P, the water status of the plants had an influence on the effect of the mucilage on K concentration in soil solution, but to a lesser extent. The difference between the effect of K addition and the exudates became smaller upon improved water supply to the plants. The change in the quality of the WSE might, as discussed before, be due to different concentration of PGA which contains most of the carboxylic groups.

To assess the relevance of the increase in soil solution P concentration due to exudation of cold- and warm-water soluble exudates, a further calculation of inflow was performed for oat (Figure 7). All input parameters in the model were the same as for the calculations shown in Figure 2 with the exception of the initial soil solution concentration (C_{Li}). This was increased by factors derived from the relations between soil solution P concentration of the controls and the appropriate treatments after adding CSE and WSE in the incubation experiments as shown in Figures 5 and 6. Just increasing C_{Li} in the calculations is a rather simple attempt to consider the relevance of exudates for P availability. Release rates of carboxylic acids, their diffusion characteristics in soil and their interactions with P are not taken into account like it is outlined in the concept of Nye (1983). However, this concept is only applicable to one specific P solubilizing compound, whereas we worked with a mixture of unknown compounds.

The effect of CSE on soil solution P concentration was small; therefore, the increase in calculated inflow was also rather small when only CSE were considered (Figure 7). Warm-water soluble exudates from plants grown at water shortage increased P concentration markedly in the dry soil, this resulted in a much higher calculated inflow. However under moist conditions, these exudates reduced P concentration in soil solution resulting in a decrease in calculated inflow. Adding both effects of CSE and WSE resulted in a fair agreement of calculated and measured inflow. The agreement was especially good at low water contents, where the initial calculations failed.

These results indicate that the ability of plants to take up more phosphate under dry soil conditions than it can be calculated by a simple diffusion model could be due to exudation of low and high molecular weight organic compounds. Furthermore, it seems that under dry conditions high molecular weight exudates are of greater importance for oat than low molecular weight exudates like organic acids. Not only the quantity of

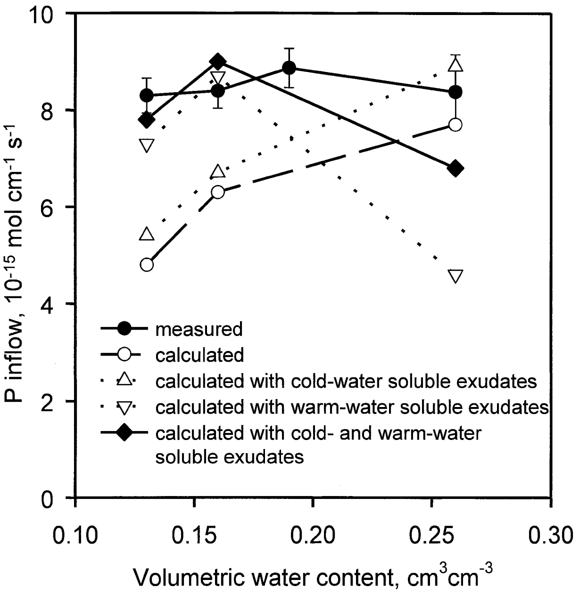

Figure 7. Comparison between measured P inflow of oat at different volumetric water contents and calculated inflows. The calculations were performed based on the measured P concentration in soil solution and increased P concentrations according to the effect of cold and warm water soluble exudates.

high molecular weight exudates was increased under dry conditions but also the quality was changed to enable the plant to counteract the negative effects of dryness on diffusion. However, conclusions have to be drawn very carefully, because the results in Figure 7 can only be rough estimates of the relevance of exudates for P acquisition for different reasons: (i) the exudates were collected under different growing conditions as compared to the growth experiment. Not only the growing medium was different, but the whole plants suffered from water and P deficiency whereas in the growing experiment the plants were only P deficient but well supplied with water. (ii) The concentration of the exudates in the incubation experiment were estimates deduced from a theoretical size of the rhizosphere and the amount of CSE collected in two hours or WSE washed away in a short time. There were no measurements of the actual concentrations of CSE and WSE in the rhizosphere. (iii) The incubation was performed at low temperature and after adding antibiotics to the soil to reduce microbial activity. It was not tested how far the activity of microorganisms was reduced. However, in an undisturbed rhizosphere microorganisms feed on root exudates, which lowers their concentration. On the other side, microorganisms are also able to change the soil chemistry and to influence the availability of nutrients. (iv) In the calculations, the improved P availability was solely explained by an increase in P concentration in soil solution. However, mucilage is also able to bind large amounts of water. In dry soils, this is of importance because it also facilitates diffusion, which can be a further beneficial effect on nutrient transport and uptake. First preliminary experiments had shown that the effective diffusion coefficient, which describes the diffusive conditions, could be higher when the soil is incubated with WSE. But unfortunately, these results were not consistent and need further investigations.

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