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Root production and root mortality of winter barley and its implication with regard to phosphate acquisition

B. Steingrobe, H. Schmid & N. Claassen
Institute of Agricultural Chemistry, Georg-August University, Von-Siebold-Str. 6, 37079 Göttingen, Germany
Tel.: +49-551-395548; Fax: +49-551-395570; email: bsteing@gwdg.de

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Abstract

Winter barley was grown in a long-term fertilizer experiment (14 years) using two P treatments: (i) no P fertilization over the whole time (−P) and (ii) an annual fertilization of 44 kg P ha^{-1} (+P). The objective of the study was to investigate the influence of the P supply on total root production and root mortality (i.e., root turnover) and to assess the benefit of a more rapid root turnover on P acquisition. Shoot development and grain yield was reduced in the '−P' treatment, whereas the standing root system had nearly the same size as in the '+P' treatment. Gross root growth was measured using the 'ingrowth core method'. Mesh bags filled with root-free soil were buried into the rooting zone (0–30 cm) and root growth into the bags over periods of 2–3 weeks was determined. Assuming that no root mortality occured inside the bags during this short period, root length in the bags will be a measure of total root production. Total root production between April and June exceeded the size of the standing root system by a factor of 2 to 3 and was significantly higher at P deficiency. Root mortality as the difference between total root production and the size of the standing root system was also increased at P shortage. P uptake was calculated by using a mechanistic transport and uptake model. Calculations based on gross root growth and root mortality resulted in a higher uptake than calculations based on the development of the standing root system, although the length of the active roots were the same in both calculations. This was due to a better exploitation of undepleted soil areas by the growing root system. The root renewal by a continuous root growth and root mortality is discussed as a mechanism of P uptake efficiency.

Introduction

Root growth pattern of plants can be influenced by the supply of phosphate. It has been shown that P shortage may increase root length (Anuradha and Narayanan, 1991), root to shoot ratio (Föhse et al., 1988), root hair density and length (Foehse and Jungk, 1983), may decrease root radius (Schenk and Barber, 1979) and alters root architecture (Liao et al., 1998). According to the authors, all these reactions are suitable to increase P uptake efficiency. However, all of these investigations were conducted on standing root systems, which are a net result of continuous gross root growth and root mortality. Gross root growth, which is the total root production, exceeds the size of the standing root system at harvest by 80% (Swinnen et al., 1995) up to 500% (Sauerbeck et al., 1980). Thus, root systems are subject to a continuous turnover and most of the roots grown during plant development are already dead at harvest.

The carbon rhizodeposition due to root mortality during plant growth was determined by van Noordwijk et al. (1994) and Swinnen et al. (1995) as 200–500 kg C ha^{-1} for wheat and barley. In pot experiments with wheat, rhizodeposition by dead roots up to harvest was equivalent to 1600 kg C ha^{-1} (Sauerbeck and Johnen, 1976). This large amount of carbon raises the question about the benefit a plant may derive from root turnover. Continuous root growth exploits a larger soil volume which might be of advantage for the acquisition of nutrients with low mobility like phosphate. Little is known about the influence of P supply on total root production or mortality. The objective of this study was, therefore, to measure gross root growth and root mortality of winter barley at different P levels and to assess the significance of the determined root

growth pattern for the P nutrition by modelling P uptake.

Root production was determined by the ingrowth core method (Steingrobe et al., 2000b) and compared to the development of the standing root system as measured by a standard auger sampling method (Böhm, 1979). The importance of gross root growth for P nutrition was evaluated by using the mechanistic model of Claassen et al. (1986, see also: Claassen, 1990; Jungk and Claassen, 1997; Claassen and Steingrobe, 1999; Steingrobe and Claassen, 2000) that describes nutrient sorption, transport towards the root and uptake by the plant. The calculations were done based on the development of the standing root system and based on the continuous root renewal given by gross root growth and root mortality.

Material and methods

Winter barley was grown in 1997 on a loamy soil in Bavaria, south Germany. It was sown at 23 September 1996 with 380 seeds m^{-2} and a row distance of 12.5 cm. Nitrogen fertilization was performed at mid April with 80 kg N ha^{-1} as stabilized ammonium sulfate nitrate. Mineral nitrogen content of the soil was 30 kg N ha^{-1} at this time. The experimental site was part of a long term fertilizer experiment. The unfertilized treatment ('−P') was without any P fertilization since 1983, whereas the fertilized treatment ('+P') received a P fertilization according to the average removal of P with the crop yield (44 kg P ha^{-1}) each year. This resulted in P concentrations in the soil of 7 and 15 mg P kg^{-1} (0–30 cm soil layer), respectively, as determined by the Ca-acetate-lactate extraction method (Schüller, 1969). Both are very low concentrations according to the German recommendation scheme for fertilization. Plot size was 20 m^2 and each treatment was replicated with four plots. The plants were not irrigated. Shoot dry matter yield, P concentration in the shoot, and root data were determined for five dates between 1 April (EC 27, end of tillering) and 18 June (EC 76, milk ripeness). Final harvest was on 22 July, but no root measurements were taken at this time.

Root measurements

For the determination of the standing root system soil cores were taken with a hand auger (two cores per plot, four plots per treatment). The cores were taken to a soil depth of 90 cm, but only the 0–30-cm layer was considered in this study. Even at harvest more than 70% of the whole root system was in the upper 30 cm. The roots were washed out of the soil carefully over a 200-μm sieve. The length was determined by a line intersection method according to Tennant (1975).

Root production (gross growth) was measured by the ingrowth core method (Steen, 1984; Hannsson et al., 1992; Majdi, 1996; Steingrobe et al., 2000b). Mesh bags (length 42 cm, diameter 4 cm, mesh wide 3 mm) were pulled over a plastic tube of the same size and inserted into the rooting zone at an angle of 45° to cover a soil depth of 30 cm. All bags were inserted at the start of the experiment and remained in the soil together with the tube until usage. At each sampling date, a set of bags was 'opened' for root ingrowth. For opening a bag, the tube was pulled out a few cm and root-free sieved soil was filled through the tube into the bag. The soil was compressed with a wooden stick to a density comparable to the average density of the bulk soil. The whole mesh bag was filled step by step with soil by repeating this procedure. The soil was taken from the same plot where the mesh bags were inserted before the experiment was conducted, sieved and stored at 4°C until usage. The average soil density was reached by weighing the soil filled into the bag according to the bag volume and the desired soil density. At each sampling date four bags per replication were 'opened' in this way for root ingrowth. At the subsequent sampling date the bags were pulled out and another set of bags was 'opened' for determining root production in the next period. Root length inside the ingrowth cores was determined as described above. Following the assumption that no root mortality occured during the short period a bag was open for ingrowth (18–23 days), the root length inside the bags characterized the root production in the respective time period. Accumulating root growth in the bags over all time periods results in total root production between 1 April and 18 June. Root mortality can be calculated from the differences in root production and the development of the standing root system.

Modelling

For calculating phosphorus uptake the model of Claassen et al. (1986) and Claassen (1990) was used (The model can be downloaded from http://www.gwdg.de/∼uaac/download.htm). This model describes: (i) the sorption of nutrients by a Freundlich function

(Steingrobe et al., 2000a)

$$\Delta C = bC_{\mathrm{L}}{}^{a} + c \tag{1}$$

where ΔC is the amount of the nutrient taking part in the diffusion, C_{L} is the soil solution concentration of the nutrient and a, b, c are fitting parameters.

(ii) massflow of nutrients (F_M) by waterflow towards the root (v_0) and nutrient concentration in soil solution (C_{L})

$$F_M = v_0 C_{\mathrm{L}} \tag{2}$$

(iii) diffusion by Fick's laws, adjusted to soil conditions

$$F_D = -D_{\mathrm{L}} \Theta f \frac{1}{b} \frac{\delta C}{\delta x} \tag{3}$$

(Parameters see below) and

(iv) net inflow (I_n) into the root by Michaelis-Menten equation.

$$I_{\mathrm{n}} = \frac{I_{\max}(C_L - C_{L\min})}{k_m + C_L - C_{L\min}} \tag{4}$$

The basic principles of this model are described by Jungk and Claassen (1997) and Claassen and Steingrobe (1999).

The input parameters for the model were determined as follows: the diffusion coefficient of phosphate in water, D_L, was taken from Edwards and Huffman (1959) ($D_L = 8.9 \times 10^{-6}$ cm^2 s^{-1}). The weight difference of fresh and dry soil gave the volumetric water content, Θ, at each date (Θ = 0.16–0.32). The impedance factor, f, was calulated from Θ according to Barraclough and Tinker (1981) (f = 0.12–0.32). Soil solution was obtained by the column-displacement method as described by Adams et al. (1980) and the P concentration in the solution was determined colorimetrically (Murphy and Riley, 1962; C_{L} = 0.41–1.04 μM (−P) and 0.67–1.37 μM (+P)). The relation between the Ca-acetate-lactate extractable P and the P concentration in soil solution at each date was taken as buffer power (b = 558–1146). Steingrobe et al. (2000a) had shown that the influence of the buffer power on uptake is minor, therefore it was not necessary to derive a precise non-linear buffer curve. Because it is difficult to get reliable values of the waterflow at root surface (v_0) in the field, the massflow was switched off in the model by setting v_0 to zero. This has nearly no influence on calculated uptake because the contribution of massflow to the total transport of P in the soil is about 1% or even less in P deficient soils (Claassen, 1990).

The average P inflow (mol cm^{-2} s^{-1}) was determined according to Williams (1948) from P uptake in a time period, average root length and time. As determined by a sensitivity analysis, the parameter of the Michaelis–Menten equation had a minor influence on calculated uptake. Therefore, the $I_{\max}$ value was set as three times the measured average influx of each period ($I_{\max}$ = 0.5–10.7 $\times$ 10^{-5} nmol cm^{-2} s^{-1}). The Michaelis constant, k_m, was set to 0.4 μM and the minimum concentration, $C_{L\,\min}$, to 0 μM (Claassen, 1990). The average root radius of each sample was measured at 20 randomly chosen root pieces under a microscope, it was not different between the treatments (r_0 = 0.11 mm).

The model also calculates uptake by root hairs. For determining root hair data, soil cores were soaked in water overnight and roots were washed out by gently agitating the buckets with the watered soil cores. One hundred root pieces of about 1 cm length were randomly chosen for root hair analysis. Each piece was placed on one side of a counting grid under a microscope and each intersection of hairs with a grid line was counted. From this the half distance between two root hairs in different distances to the root cylinder surface can be calculated to describe the root hair density in different soil layers around the root. The uptake physiology of root hairs was assumed as the same as for the root cylinder surface.

The model computes uptake of 1 cm of root length. However, a subroutine is inserted to calculate total uptake of a growing root system, if the initial root length and a root growth rate for the calculated period is given. Usually, these data are derived by taking root samples with a hand auger at the beginning and end of a period as described above. These calculations are stated in the following as based on the standing root system. For the calculations based on gross root growth, the root length determined by the hand auger was also used as initial root length. However, root growth rate was derived from gross root growth, i.e., the root length measured in the ingrowth cores. In this case root mortality must also be considered, otherwise the assumed root system in the model would be larger than in the field. Therefore, the calculated uptake was corrected by a term derived from the root mortality during the considered period and the calculated inflow of old roots.

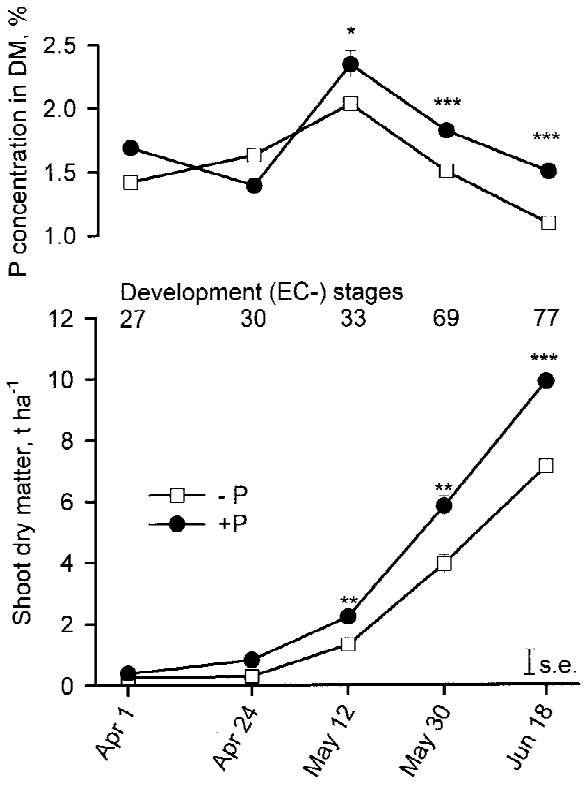

Figure 1. Shoot dry matter development and P concentration in the dry matter of winter barley grown on a loamy soil at different P levels. The '−P' and '+P' treatments had received over 14 years 0 P and 44 kg P ha^{-1} a^{-1}, respectively. No statistics were performed for 1 and 24 April. *, **,and *** denote significant differences at P = 0.05, P = 0.01 and P = 0.001, respectively. S.E. is not shown if smaller symbol size.

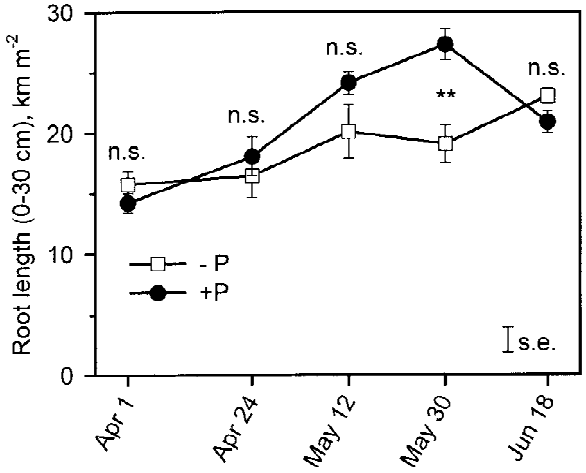

Figure 2. Length of the standing root system of winter barley (0–30-cm soil layer) grown at different P levels as determined by a hand auger sampling method. n.s., not significantly different; **significant different at P = 0.01.

Statistics

ANOVAs were performed for all data and differences between pairs of means were assessed with a Tukey test. For the first two dates (1 and 24 April) shoot material of the replications was put together for analysis. A statistical anlaysis for these dates was, therefore, not possible. Because the modelling was without replications no statistics were done comparing measured and calculated values.

Results and discussion

Shoot and root development

The higher P supply of the fertilized treatment resulted in a higher shoot dry matter production of the winter barley (Fig. 1). Grain yield at the final harvest was also increased by fertilization to 5.2 t ha^{-1} compared to 3.5 t ha^{-1} without P. With the exception of the 24 April, P concentrations in shoot dry matter were considerably lower in the '−P' treatment (Fig. 1). This suggests that the reduced yield was due to P shortage. However, compared with optimal P concentrations, which should be higher than 2.8 g kg^{-1} (Bergmann, 1993), both treatments were low in P. This is consistent with the soil P concentrations, which were also classified as very low for both treatments.

During the period of observation, the standing root systems in 0–30 cm grew from about 15 to more than 20 km m^{-2} (Fig. 2), which corresponds to 5.0 and 6.7 cm cm^{-3}, respectively. Similar root lengths for barley were found by Andrén et al. (1993). The P fertilization resulted in more roots most of the time, however, these differences were significant only at one date and less pronounced than for the shoot development. Thus, an absolute increase in the standing root length due to P shortage, as reported by Anuradha and Narayanan (1991) in nutrient solution was not observed. However, the root to shoot ratio was about 60% higher in the '−P' treatment over the whole growing period (not shown). Thus, the P deficiency seemed to decrease shoot growth to a larger extent than the development of the standing root system.

Despite the somewhat smaller size of the standing root system, gross root growth was increased under P shortage. In Fig. 3 (upper curves) the accumulated root length in the ingrowth cores is shown, which describes the total root production in the observed period. A

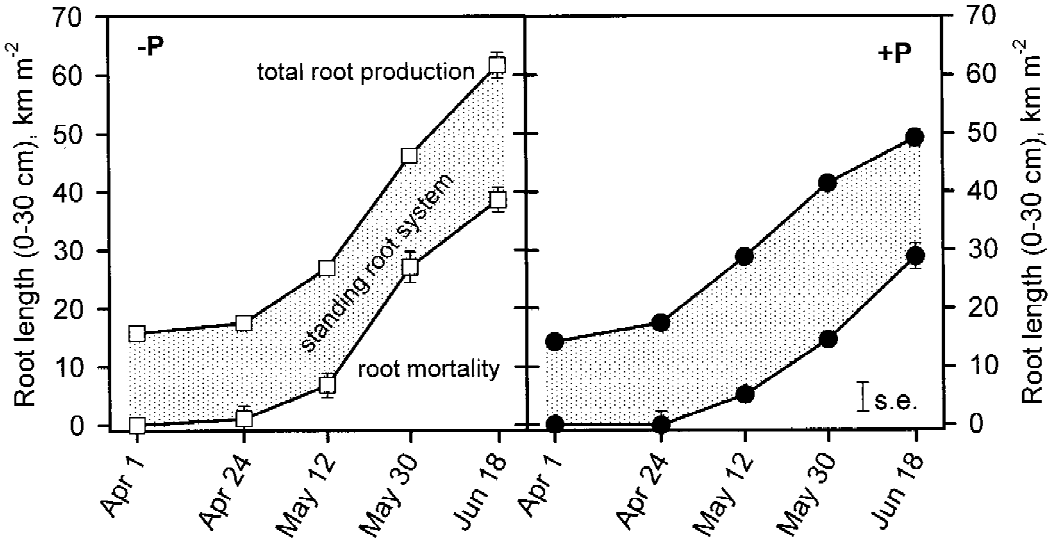

Figure 3. The total root production of winter barley (0–30-cm soil layer) grown at different P levels as determined with the ingrowth core method (upper curve). Subtracting the size of the standing root system (dotted area) results in root mortality (lower curves). s.e. is not shown if smaller symbol size.

Table 1. Root production (length and dry weight) of winter barley in relation to the shoot dry weight increment in different growing periods. The barley was grown on plots that had received over 14 years no P fertilization (−P) or 44 kg P ha^{-1} $year^{-1}$ (+P).

	Root length increment per shoot increment (m g^{-1})		Root dry weight increment per shoot increment (g g^{-1})	
	−P	+P	−P	+P
April 1–April 24	640 (55.5)	77 (6.5)[a]	2.43 (0.31)	0.29 (0.02)[a]
April 24–May 12	98 (15.9)	80 (7.1)	0.37 (0.06)	0.30 (0.03)
May 12–May 30	90 (9.9)	35 (3.5)[a]	0.34 (0.04)	0.13 (0.01)[a]
May 30–June 18	43 (3.9)	20 (2.6)[a]	0.16 (0.01)	0.08 (0.01)[a]

comparison between both treatments showed significant differences in root production during the last two periods. The shift of growing activity from shoot to root under P deficiency can be seen by the higher root production in relation to the shoot increment in each time period (Table 1). The very high value of 640 m root growth g^{-1} shoot dry matter increment was due to the slow shoot development in the '−P' treatment during April. However, besides this high value, the ratio remained higher than for the better supplied plants over the whole growing period. To assess the effort the plants made for root growth, the length values of Table 1 can be converted into root dry matter production in relation to shoot dry matter increment. Root dry matter was not measured, but was estimated assuming a specific root fresh weight of 1 g cm^{-3}, a dry matter content of 0.1 g g^{-1} (van Noordwijk and Floris, 1979) and an average root radius of 0.11 mm, which was not different between the treatments. Depending on plant age, root growth per gram of shoot increment was 0.16–2.43 g in the '−P' treatment. Hence, 14–71% of total dry matter production (shoot and root) was due to root growth. In the fertilized treatment root growth per gram shoot growth was lower at 0.08–0.30 g g^{-1}, with only 7–24% of growth devoted to roots.

The total root production of 50–62 km m^{-2} (16.7–20.7 cm cm^{-3}) as shown in Fig. 3 seems high compared to the size of the standing root system (Fig. 2 and dotted area in Fig. 3). Other data on root production of barley are scarce. Swinnen (1994) measured carbon

flow into the soil by an isotope technique and divided the total flow into carbon used for total root production including root decay and carbon in root exudates and respiration. He found amounts of 520–940 kg C ha^{-1} used for total root production of spring barley. The carbon concentration of the roots was not measured in our experiments. However, under the assumptions mentioned above (specific weight 1 g cm^{-3}, dry matter content 0.1 g g^{-1}, root radius 0.11 mm) and an assumed carbon concentration in dry matter of 0.4 g g^{-1}, the carbon input into the total root production can be estimated as 760 and 942 kg C ha^{-1}, in the same range as the findings of Swinnen (1994). Keith et al. (1986) reported a total carbon input into the soil by wheat of about 1300 kg ha^{-1}. This is higher than our estimates, but it contains not only the carbon used for total root production but also the exudated and respirated carbon.

Subtracting the size of the standing root system (dotted area in Fig. 3) from total root production resulted in root mortality (lower curves in Fig. 3). Total root mortality of the P deficient plants was also higher (39 km m^{-2}) than of the better supplied plants (29 km m^{-2}). That means 63 and 58% of the total produced roots were already dead at harvest in the '−P' and '+P' treatment, respectively. Accordingly, the size of the standing root system at harvest represented only 37 or 42% of total root production.

This large gross root growth and mortality indicate that the average root age was less than can be assumed from the development of the standing root system. This root renewal as a result of gross root growth and root mortality at a more or less constant size of the standing system was intensified at phosphate deficiency.

Similar relations between total root production and mortality have also been observed for other species. About 70% of sorghum roots (Cheng et al., 1990), 73–83% of groundnut roots (Krauss and Deacon, 1994), 56–63% of brussel sprouts roots, and 31–37% of leek roots (Smit and Zuin, 1996) died already during the study periods. All these data were determined using rhizotrons or minirhizotrons. Sauerbeck and Johnen (1976) determined a portion of about 50% of dead roots on total production for both wheat and white mustard using a carbon isotope technique. A 2–6 times larger root production than size of the standing root system at harvest was determined by Sauerbeck et al. (1980) for different plant species and growing conditions, measured also by an C-isotope technique. Thus, root production and mortality data of barley determined with the ingrowth core method were in a similar range than for other species and methods. Terefore, a large over-estimation of root production measured by the ingrowth core method due to favourable growth conditions and the lack of root competition inside the bags seems unlikely.

In contrast to our findings, Sauerbeck et al. (1980) found no influence of the P supply on root turnover of oat. Carbon loss by root respiration and root decay was 2.0 and 2.1 times higher than the amount of carbon in the standing root system for the '+P' and '−P' treatment, respectively. However, they measured the carbon distribution at an early growing stage (ear emergence), whereas in our experiment the differences in root production of barley due to P supply occured mainly at later growing stages between stem elongation (EC 33) and milk ripeness (EC 76).

Modelling P uptake

The model of Claassen et al. (1986) and Claassen (1990) calculates nutrient inflow, i.e., the amount of nutrients taken up in a time period (s) by a cm of root length, depending on nutrient transport in the soil (diffusion, sorption, massflow) and uptake physiology. An example of calculated inflow over time is given in Fig. 4a. Inflow is highest at the beginning of the calculation period or at root birth and decreases rapidly during the first days. This decrease is not due to a decrease of P uptake capacity with increasing root age as was found for barley grown in nutrient solution (Clarkson et al., 1978) because the model assumes a constant uptake physiology during the considered time period. The reason for the decreasing inflow is the depletion of P in the direct vicinity of the root surface, which can be seen by the calculated concentration profiles around the root (Fig. 4b). At the beginning of the calculations or at root birth the concentration at root surface is assumed to be equal to the soil solution concentration in the bulk soil. Due to phosphate uptake the concentration at root surface decreases, which reduces inflow according to the Michaelis–Menten kinetic (Eq. (4)). However, the decreasing concentration at the root surface increases the concentration gradient to the bulk soil and, hence, the diffusive flux towards the root (Eq. (3)). Thus, the concentration decreases rapidly until an equilibrium between both fluxes diffusion and inflow is reached, which takes several days as shown in the example given in Fig. 4. Therefore, a root system with a large portion of young roots, due to a high gross root growth, should realize a higher average inflow than a

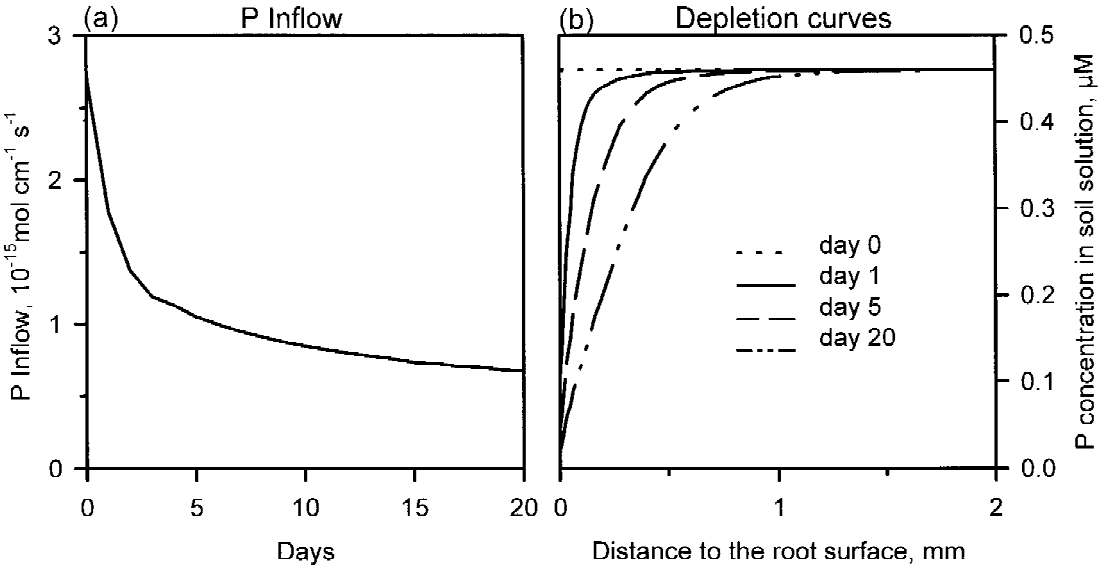

Figure 4. Calculated P inflow of winter barley as influenced by time (a) and calculated P concentration profiles around the root (b) at different time steps (depletion curves). The model input data were taken from the '−P' treatment in the time period 30 May to 18 June.

root system with low root growth, even if the size of the standing root system is not different.

To assess the relevance of gross root growth for P nutrition, model calculations were performed based on the development of the standing root system, which is the usual procedure, and based on the continuous renewal of the root system by gross growth and mortality. Figure 5 shows the results of both calculations in relation to the measured P uptake of the shoot for each time period. Measured uptake was low in April, increased rapidly and was at a maximum during the second half of May. The poor P supply of the '−P' treatment reduced measured P uptake to about a half. The calculation based on the development of the standing root system agreed well with measured uptake in April, but underestimated the measurements afterwards. Calculated uptake was only 41–74% and 61–81% of the measured one for the '−P' and '+P' treatment, respectively. It is unlikely that these discrepancies were due to wrong assumptions by determining the values of some input parameters. Sensitivity analysisses had shown that the influence of the water flow, the physiological uptake parameter, and the buffer power on P uptake is small, whereas the soil solution concentration, soil water content and root radius are more important (Silberbush and Barber, 1983; Williams and Yanai, 1996; Steingrobe et al. 2000a). These important parameters were measured at each sampling date. However, the model describes solely diffusion, massflow and sorption as transport processes in the soil. An underestimation of nutrient uptake by the model points to other processes involved in P supply (Claassen and Steingrobe, 1999). This could be, for example, the contribution of mycorrhiza to P uptake or the exudation of organic acids, which are known to increase the availability of P in the rhizosphere (Gardener et al., 1983).

In this study, we were more interested in the relevance of root renewal for calculated P uptake. Taking gross root growth and root mortality into account, the calculated uptakes increased by 4–17% in the last three periods. However, there was no difference between both ways of calculation in the first period, which was due to the very slow gross root growth during April (Fig. 3). In the time period with the highest gross root growth (second half of May) the calculated advantage in P uptake by root renewal was highest and even increased at P shortage. However, the advantage of root renewal seems less than could be expected from the course of the calculated inflow as shown in Fig. 4a. These small differences between both ways of calculation might be an artifact due to the relatively short periods of calculation. At the beginning of each calculation period the P concentration in soil solution is assumed as being evenly distributed in the soil. Therefore, calculated inflow of all roots including the older ones is high at first (refer to the example in Fig. 4). By this, calculated uptake of older roots is overestimated

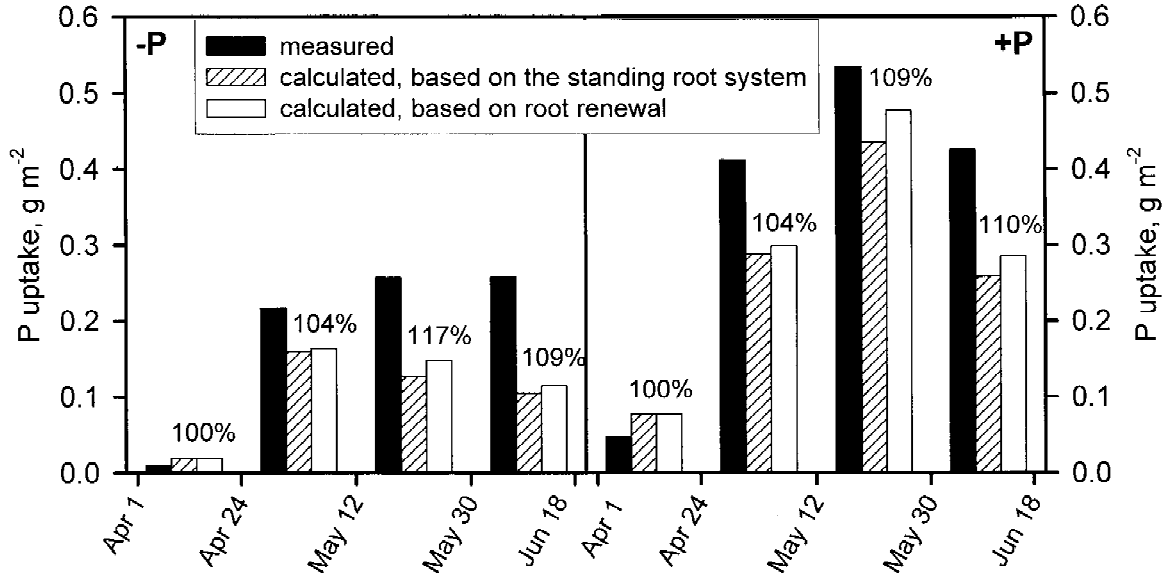

Figure 5. Comparison of measured and calculated P uptake of winter barley grown at different P levels. The calculations were based on the development of the standing root system and on root renewal. The figures above the columns denote the calculated uptake based on root renewal in relation to the calculation based on the standing root system.

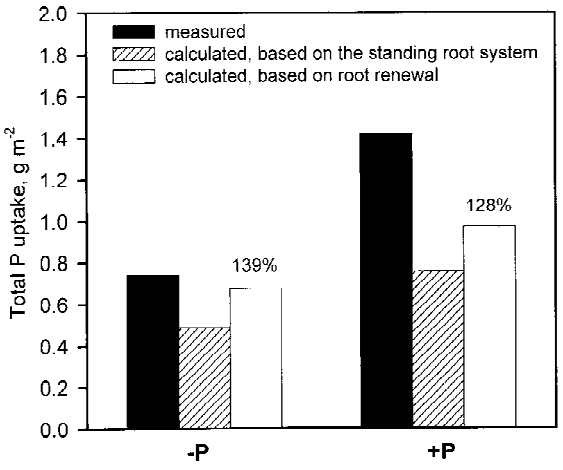

Figure 6. Comparison of total measured and calculated P uptake from 1 April to 18 June. The calculations were based on the development of the standing root system and on root renewal. The figures above the columns denote the calculated uptake based on root renewal in relation to the calculation based on the standing root system.

and, hence, the possible advantage of the root renewal is less obvious.

The subdivision into short calculation periods was done because the model assumes constancy of several not-constant input parameters like the maximum inflow, soil water content or P soil solution concentration in the bulk soil. A calculation over a long period looses accuracy. However, it would be more appropriate to assess the advantage of root renewal in soil P exploitation. A calculation over the whole time from April to June with averaged input parameters resulted in a 28 and 39% higher uptake if the root renewal is taken into account for '+P' and '−P' treatments, respectively (Fig. 6). Thus, a high root production rate could be of importance for P acquisition and the increase of root production under P shortage might be a mechanism of P uptake efficiency.

An open question still remains with regard to the increased root mortality under P shortage. Old roots are still able to take up P, although at a lower rate (Clarkson et al., 1968; Ernst et al. 1989) and at P deficiency each surplus of P uptake should be of benefit for the plant. An advantage of a high root mortality at P shortage could be a possible retranslocation of P from senescent to young roots or to the shoot. A P retranslocation from senescent leaves to the grain or young leaves was often observed (Wolswinkel, 1999), however, it is not known if such a retranslocation of P occurs also in roots. The P concentration in senescent roots of the shrub *Calluna vulgaris* and the grasses *Deschampsia flexuosa* and *Molinia caerulea* was not significantly different to young roots (Aerts et al., 1992), which denotes that no P retranslocations occurs in the root system. However, these investigations were done at a sufficient P supply. If P deficient

plants retranslocate P from senescent roots needs to be examined.

Conclusion

Root systems of winter barley are subject to continuous turnover. Even with a more or less constant size of the standing root system, roots continuously grow and die over the whole growing period. Reason for this root renewal and the benefits for the plant are still unknown. However, the increased gross root growth under P shortage indicates that root renewal is advantageous in the acquisition of nutrients when availability is low. Model calculations showed that a root system with intense gross growth and mortality exploit a larger soil volume and the calculated uptake is higher than for a constant root system with the same size. Therefore, high root turnover may be a mechanism by which the plant increases nutrient uptake efficiency. This is in addition to other well-known mechanisms such as an increased root-shoot ratio, more root hairs, or an altered root architecture.

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