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Phosphorus (P) uptake and growth of a root hairless barley mutant (*bald root barley*, *brb*) and wild type in low- and high-P soils

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ABSTRACT

The recently isolated root-hairless mutant of barley (*Hordeum vulgare* L), bald root barley, *brb* offers a unique possibility to quantify the importance of root hairs in phosphorus (P) uptake from soil. In the present study the ability of *brb* and the wild-type, barley genotype Pallas producing normal root hairs to deplete P in the rhizosphere soil was investigated and the theory of diffusion and mass flow applied to compare the predicted and measured depletion profiles of diffusible P. Pallas depleted twice as much P from the rhizosphere soil as *brb*. The P depletion profile of Pallas uniformly extended to 0.8 mm from the root surface, which was equal to the root hair length (RHL). The model based on the theory of diffusion and mass flow explained the observed P-depletion profile of *brb,* and the P depletion outside the root-hair zone of Pallas, suggesting that the model is valid only for P movement in rhizosphere soil outside the root-hair zone. In low-P soil (P in soil solution 3 μM) *brb* did not survive after 30 d, whereas Pallas continued to grow, confirming the importance of root hairs in plant growth in a P-limiting environment. In high-P soil (P in soil solution 10 μM) both *brb* and Pallas maintained their growth, and they were able to produce seeds. At the high-P concentration, RHL of the Pallas was reduced from 0.80 ± 0.2 to 0.68 ± 0.14 mm. In low-P soil, P-uptake rate into the roots of Pallas was 4.0×10^{-7} g mm^{-1} d^{-1} and that of *brb* was 1.9×10^{-7} g mm^{-1} d^{-1}, which agreed well with the double amount of P depleted from the rhizosphere soil of Pallas in comparison with that of *brb.* In high-P soil, the P uptake rates into the roots of *brb* and Pallas were 3.3 and 5.5×10^{-7} g mm^{-1} d^{-1}, respectively. The results unequivocally confirmed that in a low-P environment, root hairs are of immense importance in P acquisition and plants survival, but under high-P conditions they may be dispensable. The characterization of phenotypes *brb* and Pallas and the ability to reproduce seeds offers a unique possibility of molecular mapping of QTLs and candidate genes conferring root-hair formation and growth of barley.

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INTRODUCTION

Root hairs are outgrowths of specialized root epidermis cells, called trichoblasts. Root hair lengths and number vary amongst plant species (Föhse, Claassen & Jungk 1991) and genotypes (Gahoonia, Care & Nielsen 1997) as well as under the influence of the growth environment, especially the P supply (Bates & Lynch 1996; Gahoonia, Nielsen & Lyshede 1999). In plant nutrition root hairs are extensions of the root surface for nutrient and water uptake (Peterson & Stevens 2000), and in plant cell biology root hairs are easily accessible single cell models (Ridge & Emons 2000). The geometrical arrangement of root hairs on roots makes them very suitable for intercepting and absorbing diffusion-limited nutrients such as phosphorus (P).

Mutations that alter root-hair morphology are of special importance for understanding the role of root hairs in nutrient uptake as well as the genetic processes that precede root-hair initiation and elongation. Root-hair defective (*RHD*) mutants of *Arabidopsis thaliana* have indeed helped researchers to make progress in the genetic analysis of root-hair formation (Schiefelbein & Somerville 1990; Grierson *et al*. 1997). More recently, the *RHD* mutants have been used to study the efficiency of P uptake under various P regimes (Bates & Lynch 2000). Wen & Schnable (1994) conducted a genetic analysis of *Mutator* transposon stocks of maize for root-hair formation, and attempted to relate it to nutrient deficiency symptoms. They realized that root hairs may be dispensable under certain environment conditions, but details of the environmental conditions were not reported. The realization, that root hairs are dispensable under certain conditions and plants lacking root hairs are viable and able to reproduce normally, is useful in the creation of progeny lines, which facilitate the genetic analysis of root-hair development (Schiefelbein & Somerville 1990).

Recently, Gahoonia *et al*. (2001) characterized a root-hairless barley mutant (bald root barley, *brb*), which offered a possibility to gain knowledge on the contribution of root hairs to P uptake and plant growth. Furthermore, it

offered the opportunity to test the theory of diffusion and mass flow to predict the P depletion in rhizosphere soil with or without root hairs.

MATERIALS AND METHODS

Plant material

The spontaneous bald root barley (*Hordeum vulgare* L) mutant, *brb* and the wild-type (cultivar Pallas) were used for studying P uptake from the rhizosphere soil and in a pot experiment under controlled conditions. Originally, the mutant was found among germinating seeds of spring barley cultivar Pallas on filter papers (personal comm., Dr Thorben Lundsgaard, Plant Biology Department, The Royal Veterinary and Agriculture University, Copenhagen). Amplified fragment length polymorphism analysis (AFLP) has confirmed that the *brb* mutant has its genetic background in spring barley cultivar Pallas (Gahoonia *et al*. 2001).

Soil

The soil used in the rhizosphere studies and in the pot experiment was collected from Ap-horizont (0–30 cm) of a long-term field plot with three levels of P fertilization (0P, 10P and 20P). The soil taken from each plot was thoroughly mixed and passed through a 2 mm sieve before use. The 0P plots had received no P fertilizers since 1966. Plots 10P and 20P received 10 and 20 kg P ha^{-1} per year. To create a soil environment contrasting and limiting only in P, nitrogen (N) and potassium (K), fertilizers at rates of 120 kg ha^{-1} were applied to all the soils.

The soil has the following characteristics: clay 15%, silt 18%, sand 65%; Total C = 1.15%; Total N = 0.13%. Soil pH (0.01 M $CaCl_2$) = 5.6; cation exchange capacity (CEC) = 8.4 $cmol_c$ kg^{-1} soil at pH 7.

The concentration of soil inorganic P extractable with 0.5 M $NaHCO_3$ in the soils ($NaHCO_3$-P_i) and in the soil solution, which are considered diffusible P fractions, was as follows:

Low-P soil: Plot 0P: ($NaHCO_3$-P_i) = 14 μg P g^{-1}; soil solution P = 3 μM.

Medium-P soil: Plot 10P: ($NaHCO_3$-P_i) = 31 μg P g^{-1}; soil solution P = 6 μM.

High-P soil: Plot 20P: ($NaHCO_3$-P_i) = 46 μg P g^{-1}; soil solution P = 10 μM.

Rhizosphere studies

The *brb* mutant and Pallas were pre-grown in vermiculite filled in PVC tubes (length 100 mm, diameter 44 mm) closed at the bottom using nylon cloth that is impervious to roots (Gahoonia & Nielsen 1991). Two ceramic fibre wicks were placed along the inner sides of the tubes to supply nutrient solution of defined composition (Gahoonia & Nielsen 1992). The roots gathered at the bottom of tubes to form root mats. The tubes along with the plants (after removing the nylon cloth) having uniformly developed root mats (10 d after germination) were transferred to soil columns filled into PVC tubes (length 30 mm, diameter 56 mm). The soil columns were separated by a nylon mesh of size 53 μm (allowing only root-hair penetration) into 30 mm test soil columns below and a 1 cm soil layer above the nylon mesh. The soil columns (bulk density 1.3 g cm^{-3}) were maintained at defined moisture ($\theta = 0.22$) by placing them over small, cup-shaped sand baths each fitted with a wick dipping into a reservoir of distilled water at 20 cm water tension. After transplantation, both the *brb* mutant and Pallas developed new root mats, which completely covered the nylon mesh and represented one-dimensional root surface areas of 24.6 cm^{-2}, for exchange of solute and root exudates at the interface. The geotropic nature of root growth enabled a situation in which the 'active' apical root zones mainly remained closer to the nylon mesh (open space 22%), but in the case of Pallas, the root hairs penetrated into the soil. The experiments were conducted under controlled conditions (light intensity 280 μmol photons m^{-2} s^{-1}, light/dark period 16/8 h, temperature 18.5/15 °C, relative humidity 80%). More details of the plant growing technique and rhizosphere pH control are given in Gahoonia & Nielsen (1991, 1992). After 10 d, the soil columns were separated from the root mats, leaving the nylon mesh intact. The columns were quickly frozen in liquid nitrogen for about 1 min. The nylon mesh was removed. The frozen columns (–18 °C) were sliced with a freezing microtome (Leitz 1512; Leitz, Wetzler, Germany) to obtain rhizosphere soil samples (0.64 g soil for each 0.2 mm) at distances of 0.2, 0.4, 0.6, 0.8, 1.0, 1.5, 2.0, 2.5, 3.5 and 4.5 mm from the root mats covering the nylon mesh surface.

Determination of desorption isotherm

One gram of air-dried soil, used in the rhizosphere study, was suspended into varying volumes (ranging from 10 to 1000 mL) of 0.01 M $CaCl_2$ solutions in 2 L plastic bottles at 20 °C. The bottles were shaken by rotation in a dark room for 0.5 h daily. After 10 d, the solution was separated by centrifugation and P in the solution was measured by the method of Murphy & Riley (1962). The residual soil was dried at room temperature and it was shaken for 2 h by rotation with 0.5 M $NaHCO_3$ (pH 8.5) solution and centrifuged. The amount of P in the solution was measured as above. The relationship (desorption isotherm) between the solution P and the P extractable with 0.5 M $NaHCO_3$ is shown in Fig. 1.

To model the P concentration profiles in the rhizosphere of the *brb* mutant and Pallas, the model and procedure of Gahoonia, Raza & Nielsen (1994) was applied. The soil solution P concentration near the root mat was estimated from the desorption isotherm (Fig. 1).

The estimated values of the parameters in Table 1 and the following Eqn 1, for $x \geq \beta$:

$$c = c_i + (c_o - c_i) \exp - w(x - \beta)/D_e b \quad (1)$$

was applied to predict the expected P concentration (c) profiles of the *brb* mutant and Pallas. The symbols are explained in Table 1.

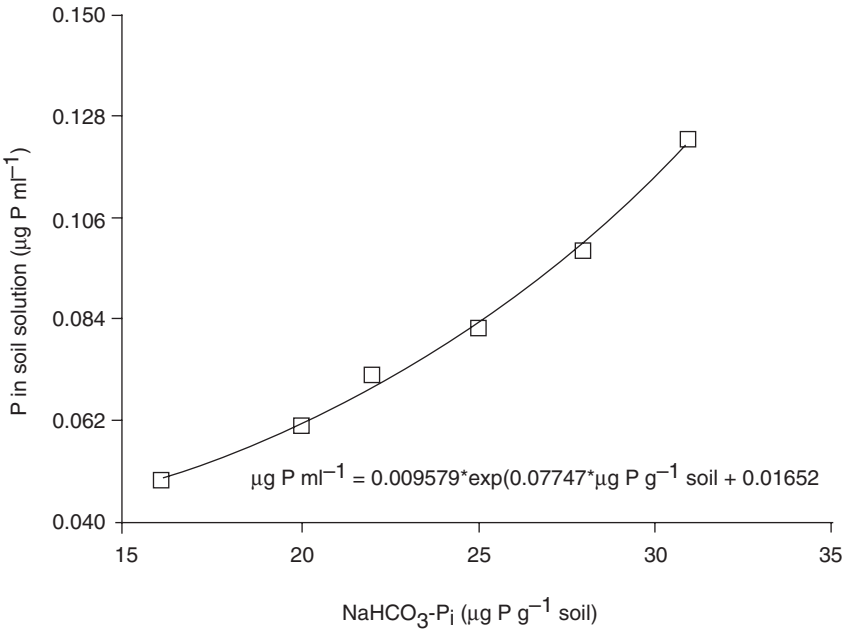

Figure 1. Phosphorus-desorption isotherm of soil (the relation between P concentration in the 0.01 M $CaCl_2$ solution and the concentration of P extractable with 0.5 M $NaHCO_3$).

Pot experiment

PVC tubes (length = 200 mm, diameter = 85 mm) were filled with 1.5 kg of soil (bulk density 1.3 g cm^{-3}) taken from the 0P, 10P and 20P plots in three replicates. Five seeds of the mutant or Pallas were sown in each tube and the tubes were placed on a sand-bath at water tension level of 20 cm to maintain equal soil moisture ($\theta = 0.22$) in each tube. After germination, the seedlings were thinned to three per pot. The plants were photographed and harvested 20 and 30 d after germination.

Determination of roots and root hairs

The PVC tubes, after cutting the shoot, were immersed in water overnight in the dark. All roots were removed carefully using a kitchen sieve. The roots, especially those of Pallas bearing root hairs, were treated in an ultrasound bath (Branson 5200; 120 W, 47 kHz; Branson Ultrasonics Corporation, Danbury, MA, USA) for 5–10 min to remove the remaining soil particles without damaging the root hairs (Gahoonia & Nielsen 1997). Root hairs on the roots of Pallas were measured using QUANTIMET 500$_+$ Image Processing and Analysis System (Leica) at 10× magnification. Some root samples of *brb* mutant and Pallas were boiled in 2.5% KOH for 3 min, washed with 1% HCl, stained with Trypan blue and examined for mycorrhizal colonization. No hyphae were seen on roots in either the rhizosphere or pot studies.

The total length of the root system and average root diameters were measured using a scanner (ScanJet IIcx) and DT-SCAN software (Delta-T Devices, Cambridge, UK).

Table 1. Estimated values of apparent diffusion coefficient ($D_e b$), rate of water flow (w), initial P concentration in the soil solution (c_i), P concentration at the surface of root mat or root-hair zone (c_o), measured root-hair length (β) and soil moisture content (θ)

Parameter	Units	Pallas	Mutant
$D_e b$	$cm^2\ s^{-1}$	0.42×10^{-6}	0.25×10^{-6}
W	$cm\ s^{-1}$	7.6×10^{-6}	7.6×10^{-6}
c_i	$\mu g\ P\ ml^{-1}$	0.1067	0.1067
c_o	$\mu g\ P\ ml^{-1}$	0.06	0.047
β	cm	0.080	0.008
θ		0.22	0.22

Root anatomy

The *brb* mutant and Pallas were grown (20 seedlings each) in sterile paper pouches covered with plastic for 7 d with nutrient supply (Gahoonia & Nielsen 1992). Root segments, 3–4 mm in length, were dissected and immediately fixed in 3% Karnavsky fixative in 0.1 M Na-cacodylate buffer (pH 7.2) for 8 h at a cool temperature. Vacuum was applied to remove air and to facilitate the penetration of the fixative into the root tissue. The tissue samples were washed with 0.1 M Na-cacodylate buffer then dehydrated with acetone series, infiltrated and embedded in Spurr's epoxy resin (Spurr 1969) and sectioned (2 μm) using an ultra-microtome (Super Nova; Reichelt-Jung, Analytical Instruments, Golden Valley, MN, USA). The sections were stained with toluidine blue (pH 9.0), mounted on glass slides, cover-slipped with oil, examined and photographed under a light microscope.

Analytical procedures

Phosphorus analysis of rhizosphere soil

To 0.5 g of air-dried soil in a centrifuge tube, 5 mL of 0.5 M $NaHCO_3$ (pH 8.5) was added (Hedley, Stewart & Chauhan 1982). The tubes were shaken for 2 h and centrifuged. Residual soil was left in the centrifuge tube, and

inorganic P ($NaHCO_3$-P_i) was determined immediately in one portion of the supernatant. For determination of total P in the supernatant, the other portion of the supernatant was autoclaved with $K_2S_2O_8$ in NaOH at 130 °C. The residual soil in the tube was dispersed in 25 mL of 0.1 M NaOH and shaken vertically for 17 h and centrifuged. Inorganic P (NaOH-P_i) in one portion of the supernatant was determined immediately. For determination of total P, the other portion was autoclaved with $K_2S_2O_8$ in NaOH at 130 °C.

The amount of P in the extracts was measured by the method of Murphy & Riley (1962). Unplanted soil samples were analysed as controls. Organic P ($NaHCO_3$-P_o and NaOH-P_o) was calculated as the difference of total P and inorganic P. The distinct uniform depletion zone due to root hairs was defined as the distance from the root mat where the measured P concentration points on the depletion profile did not differ significantly ($P < 0.05$).

Plant analyses

The shoot was cut and shoot dry weight (DM) was determined after drying at 80 °C to constant weight. The whole DM was ground and thoroughly mixed. Half a gram of DM was dry-ashed and digested in 3 M HNO_3. The amount of P in the extract was determined (Murphy & Riley 1962). Phosphorus uptake was calculated from DM and shoot P concentration.

Statistical analyses were performed using Statistical Analysis System (SAS Institute 1989) and Microsoft Excel (Microsoft Corporation, Richmond, VA, USA) as found appropriate.

RESULTS

The rhizosphere-depletion profiles of various P fractions are shown in Fig. 2. Pallas, which was bearing root hairs,

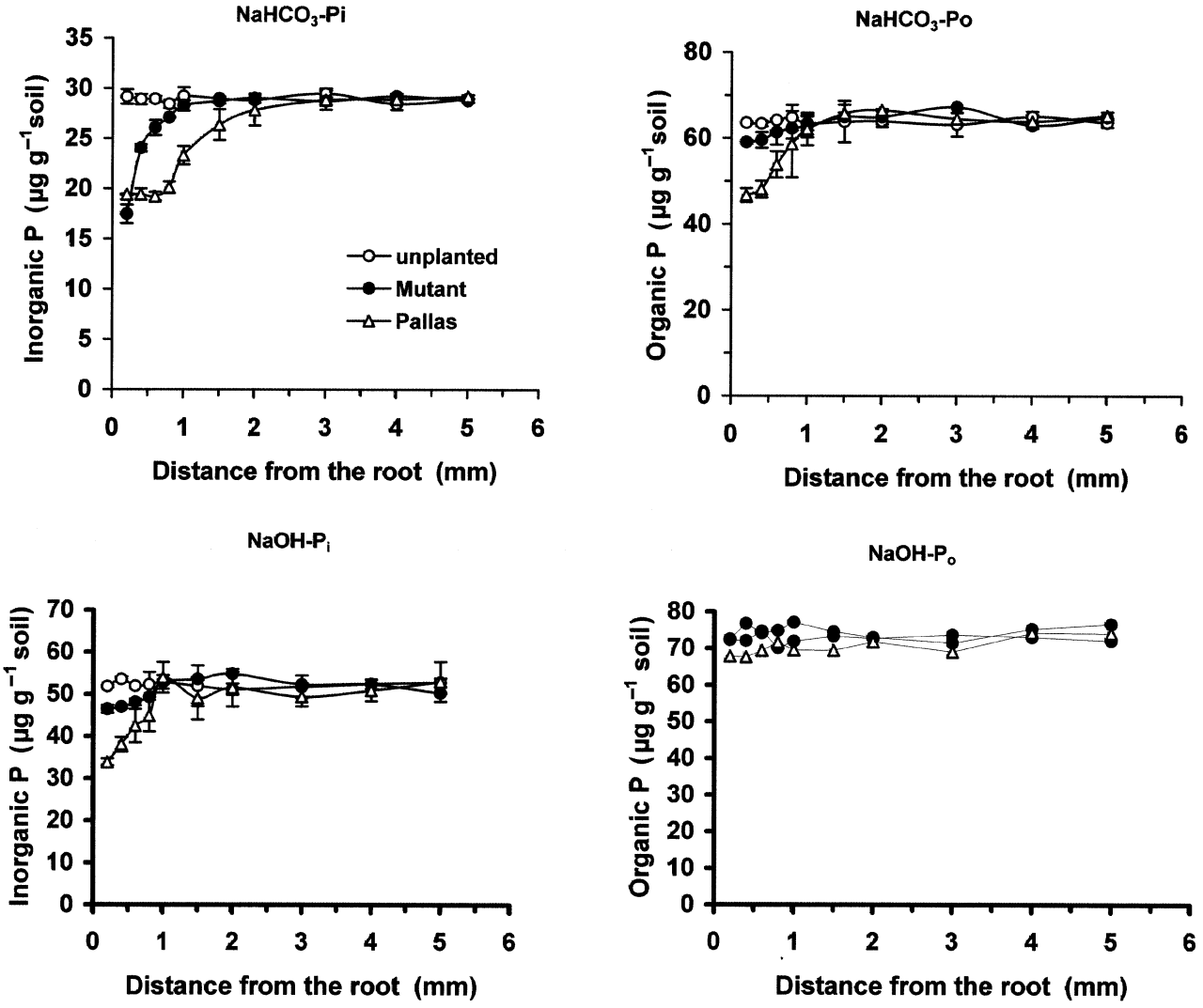

Figure 2. Depletion profiles of soil phosphorus (P) sequentially extracted, first with 0.5 M $NaHCO_3$, inorganic-P ($NaHCO_3$-Pi), organic-P ($NaHCO_3$-Po) and then extracted with 0.1 M NaOH, inorganic-P (NaOH-Pi), organic-P (NaOH-Po) in the rhizosphere of *brb* mutant and genotype Pallas.

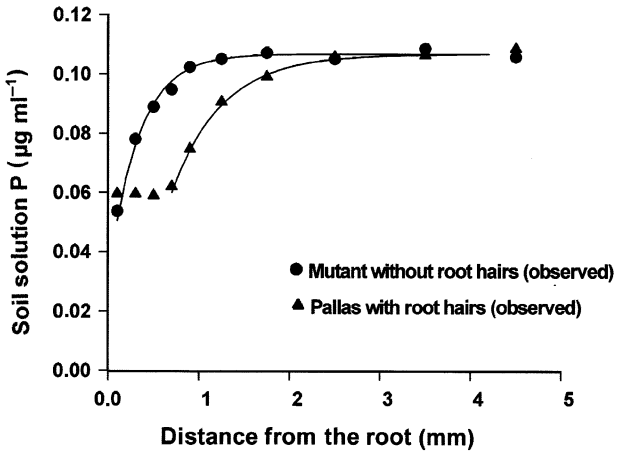

Figure 3. The estimated (symbols) and the predicted (lines) concentration profiles of soil solution P the root mats of barley *brb* mutant and the genotype Pallas.

depleted about twice as much P ($NaHCO_3$-P_i) in the rhizosphere as the *brb* mutant without root hairs. The uniform extension of the P-depletion profile of Pallas was 0.8 mm, which is equal to its root-hair length (RHL). This is consistent with the view that the concentration of a diffusion-limited nutrient, such as P, will become effectively uniform within the root-hair zone.

Pallas also depleted a larger quantity of P from a labile organic-P fraction ($NaHCO_3$-P_0) in comparison with that of mutant. This suggests that root-hair formation has a role in rhizosphere mineralization of organic P into inorganic P for plant uptake. The higher depletion of $NaHCO_3$-P_o by Pallas also indicates the relationship between root-hair formation and rhizosphere acid phosphatase (Apase) activity.

The depletion of P from less soluble inorganic-P fraction (NaOH-P_i) was also greater in the rhizosphere of Pallas in comparison with that of the mutant. Hence, root hairs may have released exudates, which induced dissolution of strongly bound inorganic-P in the rhizosphere. Neither *brb* nor Pallas depleted stable organic-P fractions (NaOH-P_o) in the vicinity of their roots.

For model calculations, the concentration of P in the rhizosphere soil solution was calculated from the relationship between $NaHCO_3$-P_i, and solution P, as shown in the desorption isotherm of the soil in Fig. 1. The observed P concentration profile in the rhizosphere of the *brb* mutant and outside the root-hair zone of Pallas agreed well with the predicted profile (Fig. 3), whereas the simple model based on the theory of diffusion and mass flow was unable to explain the observed depletion of $NaHCO_3$-P_i, $NaHCO_3$-P_o and NaOH-P_i in the root-hair zone of Pallas. This further confirmed the special role of root hairs in P uptake from soil near the root surface.

Both the mutant and Pallas grew normally up to 20 d after germination, irrespective of soil P levels. After this period, the *brb* mutant began to develop P-deficiency symptoms. In low-P soil (0P, soil solution P = 3 μM), *brb* mutant plants virtually died after 30 d, whereas Pallas continued to grow (Fig. 4), in spite of the similar specific root lengths (m g^{-1}) of both the mutant (82 ± 3.0) and Pallas (85 ± 4.0) and similar root anatomy (Fig. 5). This shows the impor-

Figure 4. Growth of barley mutant (*brb*) without root hairs and genotype Pallas with root hairs in low-P (0P) and high-P (20P) soils 30 d after germination.

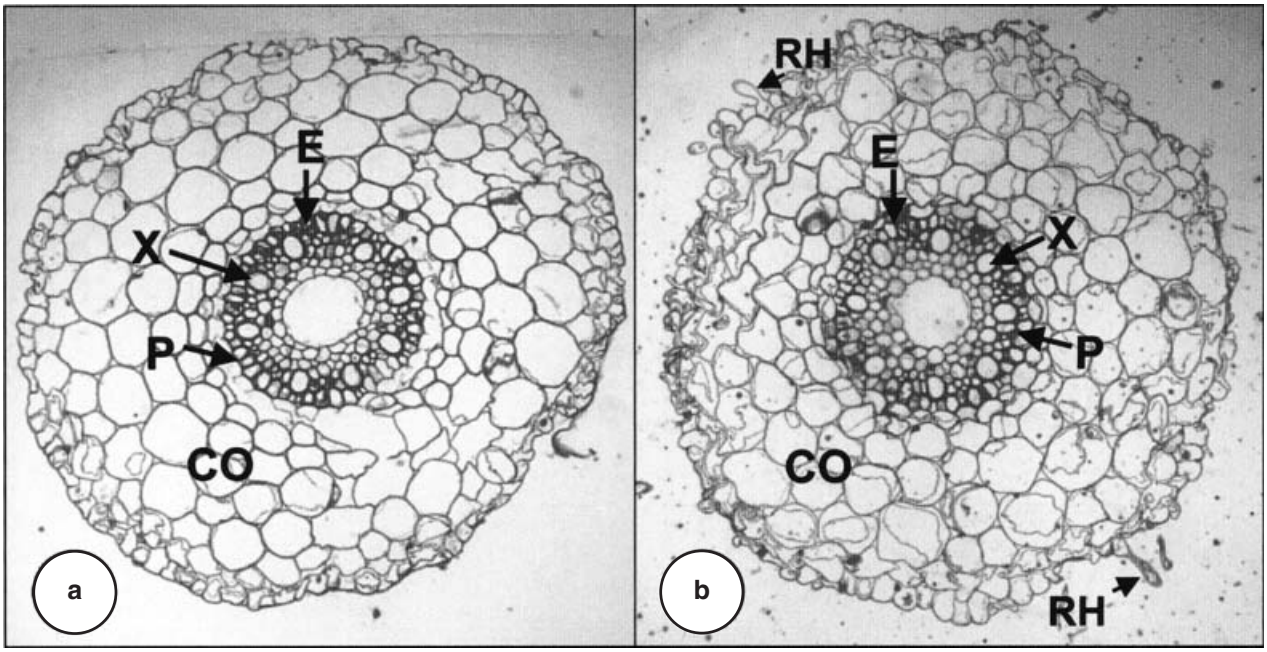

Figure 5. Root anatomy of bald root barley, *brb* mutant (a) and the wild-type, barley genotype Pallas (b). Transverse sections (250×), root hairs (RH), cortex (CO), pericycle (P), endodermis (E) and xylem vessel (X).

tance of root hairs for plant growth in a P-limiting soil environment. In high-P soil (20P, soil solution P = 10 μM) both the mutant and Pallas maintained their growth, although the *brb* mutant (0.98 ± 0.10 g pot^{-1}) produced non-significantly less shoot biomass than Pallas (1.06 ± 0.11 g pot^{-1}). Hence, root hairs may be dispensable for plant growth in a high-P environment, in which better P diffusion in blend with the reduced RHL may render the benefit from root hairs less valuable.

In low-P soil, the mean rate of P uptake by Pallas per unit root length and time was 4.0×10^{-7} g P mm^{-1} d^{-1} and that of *brb* was 1.9×10^{-7} g P mm^{-1} d^{-1} (Fig. 6). Thus the uptake rate of P by Pallas was twice as high as that of the *brb* mutant, which is supported by the data in Fig. 2 showing considerably higher P depletion by Pallas than by *brb*. The shift from low-P soil to high-P soil increased the uptake rate of Pallas by 1.4 times to 5.5×10^{-7} g P mm^{-1} d^{-1}. The increase in *brb* was 1.7 times to 3.3×10^{-7} g P mm^{-1} d^{-1}. Here also it is evident that root hairs are more important in low-P soils, because the presence of root hairs improved the P uptake rate of Pallas versus the *brb* mutant more in low-P (2.1 times = 4.0/1.9) than in high-P (1.7 times = 5.5/3.3) soils. One of the reasons for the smaller increment in P uptake rate of Pallas in high-P soil is that the increase in P level reduced RHL (Fig. 7). The RHL (mm) in low-P soil was 0.8 ± 0.21 in comparison with 0.68 ± 0.14 in high-P soil. Hence, the loss of increment (1.4/1.7 = 0.82) in P-uptake rate can be fully explained by the decrease in RHL (0.68/0.8 = 0.81).

DISCUSSION

The significance of root hairs in P uptake and growth was investigated by using phenotypes (barley cultivar Pallas and its *brb* mutant), which differed only in root-hair formation and were otherwise indistinguishable from each other. The agreement in results of the rhizosphere studies (one-dimensional root–soil contact), modelling (diffusion and mass flow theory) and the pot experiment (cylindrical root–soil contact) has confirmed the considerable contribution of root hairs in P uptake and growth of barley in low-P soil. This agrees with the results of previous studies with *Arabidopsis thaliana* (Bates & Lynch 2000). The extent of the $NaHCO_3$-P_i-depletion zone close to the roots of Pallas was extended by root hairs (Fig. 3). Because of densely clus-

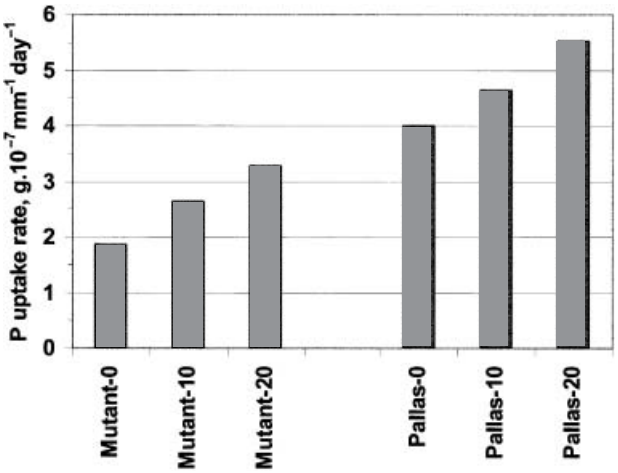

Figure 6. Phosphorus uptake rates of barley mutant (*brb*) and genotype Pallas in soil at three P levels. (0P = no P since 1966, soil solution P = 3 μM; 10P = 10 kg P ha^{-1} year^{-1}, Soil solution P = 6 μM; 20P = 20 kg P ha^{-1} year^{-1}; soil solution P = 10 μM).

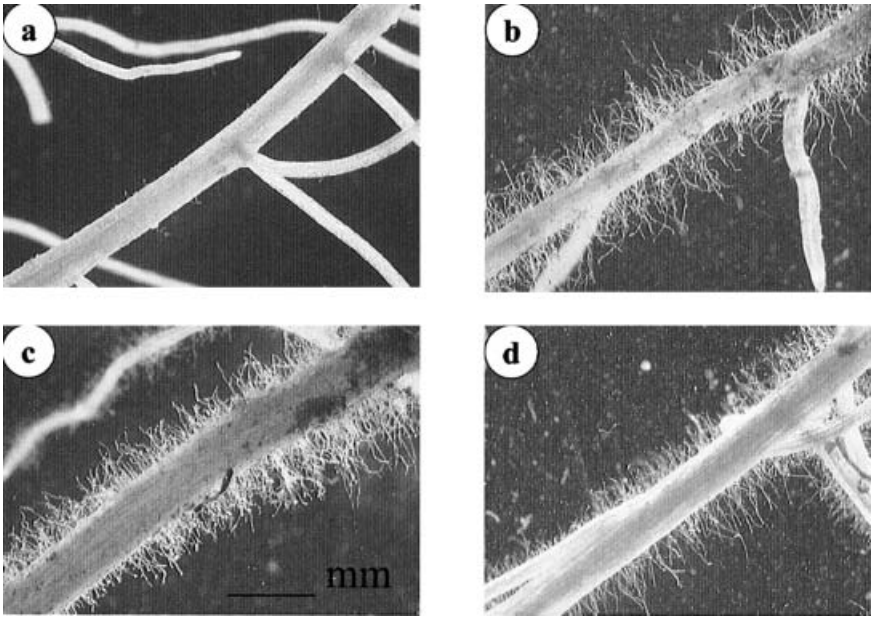

Figure 7. Root-hair formation of barley *brb* mutant (a) and genotype Pallas, in 0P (b), in 10P (c) and in 20P (d). (0P = no P since 1966, soil solution P = 3 μM; 10P = 10 kg *P* ha^{-1} $year^{-1}$, Soil solution P = 6 μM; 20P = 20 kg *P* ha^{-1} $year^{-1}$; soil solution P = 10 μM).

tered root hairs (Fig. 5b), the concentration of diffusion-limited nutrients such as P within the root-hair cylinder became effectively uniform (Nye 1966; Tinker & Nye 2000) and the competition amongst root hairs for P created the distinct uniform depletion zone near root surface. The applied model (Eqn 1) predicted the $NaHCO_3$-P_i concentration profile in the rhizosphere of Pallas only beyond the distinct uniform depletion zone created by root hairs (Fig. 3), which may be one of the reasons for underestimation of P uptake by models (Itoh & Barber 1983; Föhse *et al*. 1991) when the role of root hairs is not fully included, for example, the depletion of $NaHCO_3$-P_o and NaOH-P_i (Fig. 2). Additionally, Pallas roots with root hairs also appeared to induce higher rhizosphere activity of acid phosphatase (Dosier & Riopel 1977; Gahoonia *et al*. 2001), which may contribute to the mineralization of P from organic pools. The model simulation by Hoffland (1992) suggested the release of organic acids such as citric acid by root hairs, which potentially increased the dissolution of the strongly bound P pools in the rhizosphere as observed for Pallas in contrast to that of *brb* mutant (Fig. 2; NaOH-P_i).

The P-depletion profiles in the root mat study and P-uptake rates in the pot experiment were determined after similar growth periods of 20 d after germination. In the pot experiment, root hairs doubled the P-uptake rate into the roots of Pallas in comparison with that of *brb* mutant (Fig. 6), which explained the twice-greater depletion of $NaHCO_3$-P_i in the rhizosphere of Pallas (Fig. 2). In both the experiments, the same soil, amended to three different P levels, was used and, in particular, soil moisture conditions ($\theta = 0.22$) were kept identical, as otherwise they might have confounded the results due to a change in P diffusion (Barraclough & Tinker 1981) and root-hair length (Schnall & Quatrano 1992). The *brb* mutant did not form root hairs under any condition of the present experiments (Fig. 7) and unlike the previous study with *Arabidopsis* root-hair mutants (Tanimoto, Roberts & Dolan 1995) the ethylene treatment could not reverse the lack of root hairs on the *brb* mutant roots (Gahoonia *et al*. 2001). Barraclough (1986) calculated that with soil solution concentration below 8 μM P, the transport of P through soils can be a growth-limiting factor. Hence, the used low-P soil (0P) with 3 μM P in soil solution can be considered a P-limiting growth environment, and the high-P soil (20P) with 10 μM P in soil solution a non-limiting growth environment.

In agreement with the studies with *Arabidopsis* (Bates & Lynch 1996), *Phaseolus vulgaris* L. (Yan & Lynch 1998) and with *Brassica napus* L and *Spinacea oleracea* L. (Föhse & Jungk 1983) the RHL of barley was greater in a low-P environment (Fig. 7). Hence, the response of RHL to a low-P supply appears to be general. The reason for the greater RHL of barley in low-P soil is not known, but in *Arabidopsis*, the regulation of RHL by P supply was associated with the changes in cytosolic pH (Ma *et al*. 2001).

CONCLUSIONS AND PERSPECTIVES

The root-hair formation and its plasticity with P supply is an important mechanism for adaptation and survival of plants in low-P soil environments. When challenged by a low-P supply, Pallas extended its RHL to intercept diffusing P, and probably also induced other root-hair promoted rhizosphere processes, such as the release of organic acids and acid phosphatase, to acquire P, whereas, the *brb* mutant without root hairs was devoid of these advantages and died. The theory of diffusion and mass-flow describes the development of P concentration profiles near plant roots only outside the root-hair zones or when the roots are considered 'smooth' cylinders. The information is useful for fine-tuning the models of nutrient uptake, and for plugging the knowledge gap leading to the discrepancies between predicted and measured values. The characterized phenotypes,

brb mutant and Pallas for P uptake, differed only in root-hair formation and both the phenotypes grew and reproduced normally with high nutrients supply, offering the opportunity to create progeny lines for mapping QTLs and searching candidate genes of root-hair formation in cereals. Such knowledge, together with the vast variation found in root-hair formation of cereal and legume genotypes, can provide a basis for breeding new P acquisition-efficient genotypes for extending the limited life period of world P resources.

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