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Barley genotypes with long root hairs sustain high grain yields in low-P field

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Abstract

Superior root traits, like long root hairs, enhance phosphorus (P) uptake and hence the selection for root hair trait offers the possibility to sustain yields in low-P soils. It is yet unknown whether root hair promoted P uptake of barley genotypes is related to the grain yield in low -P field soil. To investigate this, a set of barley genotypes was pre-screened using hydroponics for long (about 1 mm, cvs. Pongo, Linus Barke, Tofta, Henni) and short root hairs (about 0.5 mm, cvs. AC91/5606/17, Meltan, Scarlett, Century, Otira, and Cecilia). The selected genotypes were cultivated in low-P field plots (no P in 35 years, 3 μM P in soil solution) and in plots amended by moderate (10 kg P ha^{-1}, 6 μM P in soil solution) and high (20 kg P ha^{-1}, 10 μM P in soil solution) P fertilisation. The ranking of the genotypes root hairs in laboratory remained consistence in the field, except for cv. Barke (1.05 mm). The genotypes varied in specific root length (SRL, m g^{-1}) and root hair length (RHL), but the estimated volume of soil explored by root system clearly depended on RHL. The correlations of RHL ($R^2 = 0.60^{***}$), volume of soil explored by root system ($R^2 = 0.57^{***}$) and SRL ($R^2 = 0.40^{**}$) with the P uptake in the field were highly significant. The correlation of root-shoot ratio with the P uptake was non-significant ($R^2 = 0.11$). The genotypes with long root hairs preserved economical stable grain yield in low, moderate and high P plots. In contrast, the genotypes with short root hairs produced lower grain yield in low P soil, but they responded to moderate and high P fertilisation by significant increase in their grain yields. From the results of this field-based case study, it is concluded that barley genotypes with long root hairs are better adapted in low P soils and they express high yield potentials both in low and high P soils.

Introduction

Phosphorus (P) deficiency in crop production is prevalent. Conventionally, fertilizers or manure amendments are used to counteract the deficiency. There is valid concern that fertilizer alone cannot sustain yields for long periods (Tilman et al., 2002), because of (a) P being non-renewable resource, (b) the inability of many farmers to buy enough fertilizer, and (c) the capacity of many soils to bind applied P into forms unavailable to plants (Sanchez and Leakey, 1997). Although many soils are not actually low in total P, Abelson (1999) projected likelihood of a potential phosphate crisis for agriculture in the 21st century. To counteract the anticipated P shortfall, scientists need to discover mechanisms in plants that enhance P acquisition and exploit them to make plants more efficient at acquiring P, search and develop P-efficient germplasm, and optimise crop management schemes that increase bioavailability of soil P. Among the alternative measures is the possibility of selection and breeding for P efficiency, which holds a potential to reduce level of P fertilisation in developed countries and sustain high yield in P-fixing soils of developing countries. The potential value of the measure is reflected by the fact that low level of available P in the soil solu-

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tion leads to numerous morphological, physiological, biochemical and molecular adaptations by plants for acquiring P (Raghothama, 1999). The root to shoot ratio of plants increases under P stress and the root diameter decreases, while the size of absorptive surface area relative to root volume increases for Pi acquisition (Lynch, 1995). In addition to increased root growth, production and elongation of root hairs also increase under P deficiency (Bates and Lynch, 1996). The presence of root hairs increases the P-absorbing area per unit length of root and the significant role of root hairs in P acquisition is well documented in laboratory (Gahoonia and Nielsen, 1998) and under field conditions (Gahoonia et al., 1999). Recent studies (Gahoonia et al., 2001), based on the segregation ratio of 1.3 in F_2 generation of cross between root hairless mutant *brb* and its wild type (spring barley cultivar, Pallas) suggested that root hair trait followed the simple Mendelian mode of Inheritance. Although the systematic studies have confirmed the role of long root hairs in higher P uptake and above ground biomass production, it remained unclear, whether the superior P uptake of barley cultivars with long root hairs is related to grain yield in the low P field with and without P applications? Such knowledge is essential; because breeders, farmers and society would be interested in the cultivars able to produce economical and stable grain yields in low P soils and with little P applications, as a practical indicator of P efficiency and for minimizing the negative effect of P fertilization on environment.

The potential yield ceiling of barley genotypes may differ, because they are often bred for given traits with focus on malting quality or feed and fodder. Therefore, it is often difficult to draw meaningful conclusions on P efficiency and its relation to grain yields by comparing the genotypes only at low P levels. The genotypes, expressing maximum yield potentials in P limiting as well as in high P (non-limiting) soils, are envisaged of special value in selection and breeding of new P efficient barley genotypes. In this paper we report a relationship of root hairs promoted P uptake of selected barley genotypes to the grain yields in P limiting soil and when the soil was fertilised with moderate and high P applications.

Materials and methods

Laboratory screening of cultivars

Thirty-eight spring barley genotypes were grown using hydroponics (Gahoonia and Nielsen, 1997) and pre-screened for root and root hairs formation. Based on the detected variation in root system and root hair formation, the following genotypes were selected for field study. The genotypes Pongo, Linus Tofta, Henni, had long root hairs. The barley genotypes, AC91/5606/17 (AC/91), Barke, Meltan, Scarlett, Century, Otira, and Cecilia had shorter root hairs on their roots in the laboratory studies.

To avoid persistence holes in the research field plots, the size of root system was studied only by nutrient solution experiment. Root hairs were studied both in the solution culture and in the field as described below.

Plant growth

To measure roots and root hairs in a nutrient solution culture, the plants (three replicates) were grown in five-litre pots containing low P (10 μM) otherwise complete nutrient solution (Gahoonia and Nielsen, 1997). Its electric conductivity was maintained at 0.63 mS cm^{-1} by addition of maintenance solution, according to a pre-determined relationship between volume added and electric conductivity and the solution pH was maintained at 5.5 ± 0.2 by addition of ammonium or nitrate solutions (Gahoonia and Nielsen, 1992); in order to keep solution pH close to that of the soil (pH 5.6) in field experiment. To minimise the effect of aeration position on root hair development (Ewens and Leigh, 1985), all the pots were aerated by placing an air tube in the middle at the bottom.

Root length and root hair determination

When the plants were 21 days old, six randomly selected root segments (about five cm long) from each replicate were placed in a film of water in petri dishes. Root hair images were captured for all the cultivars on the main root axis, first order and second order roots, using a video camera fitted to a microscope interfaced with a computer image grabber board. Root hairs and root diameter were measured by recalling the images using Quantimet 500_+ Image Processing and Analysis System (Leica) at $10\times$ magnification. Root hair length (RHL) was measured at 10 randomly selected places covering the entire root segment. The root hair lengths of all the root segments were averaged, which adequately described the volume of soil exploited by the

root hairs. Determination of root hair density (RHD) was not reliable due tangling of especially long root hairs, hence only pictographic assessment of RHD was done and presented in Figure 4. The length of the root system (including root segments after root hair determination) was measured using a scanner (ScanJet IIcx) and *Dt-Scan software* (Delta-T Devices, Cambridge, England). All laboratory experiments were conducted under controlled conditions (light intensity 280 μE $s^{-1}m^{-2}$, light/dark period 16/8 h, temperature 18/15 °C, and relative humidity 75%).

Field experiment

Experimental design

A complete randomised design with four replicates was used. Two replicates were harvested for determination of grain yield and the rest two replicates for determination of P uptake and above ground biomass production. Gauch and Zobel (1996) argued that in selection experiments, the net selection gain with two replications is only slightly reduced from optimum selection net gain with three replications. The plot size was 1.5 × 10 m. The experimental site was located on a sandy clay loam in Denmark. There were three phosphorus applications (0P, 10P and 20P). The 0P plots received no P fertilisers since 1966. Nitrogen (N), phosphorus (P) and Potassium (K) fertiliser applications (kg ha^{-1}) to the plots were as follow: *Plot 0P*: 60N, 0P, 60K; *plot 10P*: 60N, 10P, 60K; *plot 20P*: 120N, 20P, 120K.

The treatment 120N, 20P, 120K allowed the assessment of the expression of genetic variation in grain yields and yield potential of the genotypes with fertiliser applications close to that of non-limiting conventional fertilisation practices. The P and K fertilizers were applied about six months before sowing and they were mixed to soil by ploughing. The N fertiliser was applied a week before sowing. White clover was growing on the experimental site in the previous year.

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. *Plot 0P*: soil inorganic P extractable with 0.5 *M* $NaHCO_3$ ($NaHCO_3$-P_i) = 0.45 mmole P kg^{-1}; soil solution P = 3 μM. *Plot 10P*: $NaHCO_3$-P_i = 1.0 mmole P kg^{-1}; soil solution P = 6 μM. *Plot 20P*: $NaHCO_3$-P_i = 1.5 mmoles P kg^{-1}; soil solution P = 10 μM. 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 P-limiting environment and medium P soil (10P) with 6 μM P in soil solution as moderate P-limiting and the high-P soil (20P) with 10 μM P in soil solution as non-limiting growth environment. Chemical spraying controlled pests, diseases and weeds.

Soil phosphorus was extracted with 0.5 *M* $NaHCO_3$, pH 8.5 (Olsen et al., 1983) and determined by the method of Murphy and Riley (1962). Soil solution was obtained by displacement (Adams, 1974).

Sampling of plant material

To check the uniformity of germination, number of plants in one-meter row was counted at two places in each plot. The small variation (21 ± 1.6) indicated uniform germination. For determination of P uptake and above ground biomass production, aerial parts (DM) from 1 m^2 per plot were harvested 5 times during the growth period after 30, 40, 52, 65, 87 days after germination. In this paper, P uptake at 87 days (close to the grains harvest) was used and it was related to the grain yields.

Plant chemical analysis

Shoot dry weight (DM) was determined after drying at 80 °C to constant weight. Whole DM was ground and thoroughly mixed. One gram DM was ashed at 500 °C and digested in 3 *M* HNO_3. P in the solution was determined (Murphy and Riley, 1962). Phosphorus uptake was calculated from DM and P concentration.

Root hair determination

For root hair determination on field grown roots in low-P plots (0P), soil cores with intact plants and roots were taken up to about 10 cm soil depth (3 replicates, 30 days after germination) with a knife. The soil cores were immersed in water overnight in darkness at 5 °C. The roots were then removed carefully using a kitchen sieve and subjected to an ultrasound treatment (120W, 47k Hz) in Ultrasound bath (Branson 5200) for 5–10 min to remove remaining soil particles without damaging the root hairs. Root hairs were measured using image analysis as described above. A part of the roots sampled at 30 days after germination were boiled with 2.5% KOH for 3 min, washed with 1% HCl, stained with Trypan blue. Mycorrhizal colonisation was not detected. Root hair formation of all cultivars, except Barke, was consistence between

laboratory and field experiments. Barke had shorter root hairs (0.78 mm) in nutrient solution experiment as compared to long root hairs (1.05 mm) in the field experiment. As compared to other genotypes with short root hairs, Barke can be still ranked as a genotype with long root hairs. Assuming the similar relative ranking of root length of genotypes in nutrient solution experiment and in the field, the field data of root hairs was used for estimation of soil volume explored by root hairs.

Calculation of soil volume explored by root hairs

The calculation of soil volume exploited (V) by root system with root hairs was calculated as followed, adapted and corrected from Gahoonia and Nielsen (1997),

$$V = \pi(\zeta^2 + 2\zeta r)L, \quad (1)$$

where ζ is root hair length, r is root radius and L is root length.

The standard deviation for V was calculated according to the rules of multiplication and addition of variance, as:

$$S.D./V = \sqrt{\pi \frac{2\frac{v_\zeta}{\zeta} + 2\left(\frac{v_\zeta}{\zeta} + \frac{v_r}{r}\right)}{\zeta^2 + 2r\zeta} + \frac{v_L}{L}},$$

where v_ζ is variance of measured root hair length, v_r is variance root radius and v_L is variance of root length.

Statistical analyses were performed with Statistical Analysis System (SAS) Institute, (1989) and Microsoft Excel software as found appropriate.

Results

The results presented in Figure 1 show that the investigated spring barley cultivars differed in root hair length (RHL, mm), volume of soil (cm^3) explored by the root system, specific root length (SRL, m g^{-1}), root-shoot ratio (cm mg^{-1}). The RHL (mm) of Pongo (1.34), Linus (1.30), Barke (1.05), Tofta (0.91) and Henni (0.91) is above or close to one mm (1-mm group) and AC/91 (0.61), Meltan (0.57), Scarlett (0.56), Century (0.54), Otira (0.46) and Cecilia (0.40) have RHL close to 0.5 mm (0.5 mm group). The volume of soil explored by root hairs on the root system of a given genotype was clearly the function of the RHL. Pongo with longest RHL and longest SRL explored largest volume of soil. Linus with high RHL, despite the short SRL ranked second in exploring the soil volume. The correlation of RHL ($R^2 = 0.60^{***}$), volume of soil explored by root system ($R^2 = 0.57***$) and SRL ($R^2 = 0.40^{**}$) with the P uptake in the field was highly significant (Figure 2). The correlation of root-shoot ratio with the P uptake was non-significant, suggesting that the spatial distribution of root system rather than total carbon investment into the roots is important for P uptake.

The genotypes with RHL in 1-mm group did not increase P uptake with the increase in P levels from OP to 20P (Figure 3). Pongo absorbed 20 kg P ha^{-1} in low-P soil, which remained without P applications (no-P) since 1966 and its P uptake did not increase with the fertiliser applications of 10 and 20 kg P ha^{-1}. Similar was the case with other cultivars (Linus, Barke, Tofta and Henni) having long root hairs. The P uptake of the cultivars with RHL in 0.5 mm group increased when the soil P levels were increased by P fertiliser applications. For example, Cecilia with shorter RHL (0.4 mm) absorbed 13 kg P ha^{-1} in no-P soil, but it increased to 20 kg P ha^{-1}, when 20 kg P ha^{-1} was applied. Among the short root hair cultivars, AC/91 and Otira absorbed relatively high amounts of P as compared to other cultivars in the group. This is because of the highest SRL of AC/91 among all the cultivars investigated and the longest RHL among the cultivars with short root hairs, which resulted in greater volume of soil explored for P in low-P soil. In contrast to all other cultivars, Otira appeared to possess the ability to acidify its rhizosphere as revealed by yellowish colour near roots (data not shown) embedded in Agar containing indicator dye Bromocresol purple (Marschner and Römheld, 1983). The acidification might have helped it to mobilise more P especially in low-P soil.

The cultivars with long root hairs (1 mm group) maintained the high grain yield in low (0P), moderate (10P) and high (20P) P supply (Figure 4). For example, Pongo and Linus produced about 5.8 tons grain ha^{-1}, irrespective of P application. Although RHL of Barke differed somewhat between solution culture (0.78 mm) and field (1.05 mm), it is more close to 1-mm group. Barke produced 7 tons grain ha^{-1} in soil without P application (0P) for about 35 years and P fertilisation showed no response to the yield. In contrast, the cultivars with RHL in 0.5 mm group produced lower grain yield in low P soil, but they responded to moderate and high P fertilisation by significant increase in their grain yields. It is evident from the data, that good malting and high yielding cultivars, like Meltan and Scarlett having short root hairs, do

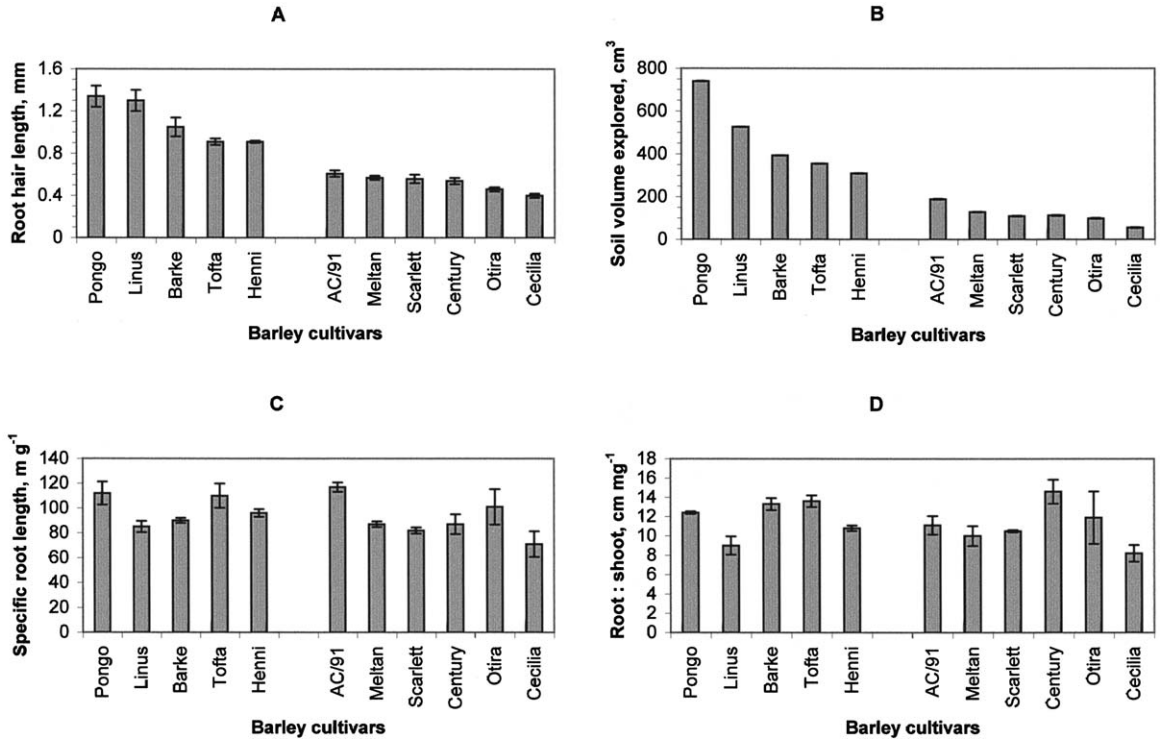

Figure 1. Root hair length (A), estimated soil volume explored (B), specific root length (C) and root: shoot ratio (D) of barley genotypes. The error bars represent the *LSD* at the 5% level.

not express their full grain yield potential in low P soil, but when P fertilisers are applied they reached the yield potential of about 7 tons ha^{-1}. This advocated that the low-P field soil (0P) actually represented the yield-limiting low P environment.

Discussion

The role of root hairs in P uptake and plant survival has been demonstrated in many previous studies with many plant species and root hair mutants (Föhse et al., 1991; Bates and Lynch, 2000; Gahoonia and Nielsen, 2003; Yan et al., 1995). The results of the present study showed that the long root hairs of barley contributed to obtain stable grain yield in both P limiting and P non-limiting soil environments.

The barley cultivars were pre-screened for RHL under laboratory conditions to perform the targeted field study. The ranking of the investigated genotypes for RHL was consistence (slight deviation with Barke) under laboratory and field conditions also observed in previous studies (Gahoonia and Nielsen, 1997). The variation in RHL was concomitantly related to the P uptake (Figure 3) and the grain yield (Figure 4). Grain yield is a complex trait and the potential of a given genotype to produce grains in given environment may differ due to the yield components, like number of kernels per spike, thousand kernels weight (Egle et al., 1999) and tillering capacity (Rodriguez et al., 1998). In the present study, only grain yield, the end result of the components, was determined. The cultivars with longest RHL, e.g., Pongo and Linus, though did not produce absolute highest grain yield (due to lower grain yield ceiling), but their longer root hairs certainly contributed to maintaining the high and stable grain yield, regardless of P limiting or high P conditions in the soils (Figure 4). Laboratory (Bates and Lynch, 1996; Föhse and Jungk, 1983) and field studies (Gahoonia et al., 1999) have shown that plants adapt to low P supply by extending the length of root hairs. Such plascity help them to explore larger volume of soil for P acquisition, especially in the low-P soils.

Application of P fertiliser reduced the length of root hairs in the field (Gahoonia et al., 1999) and furthermore the improved diffusion of P at high P supply renders the benefit of root hairs less valuable in P uptake.

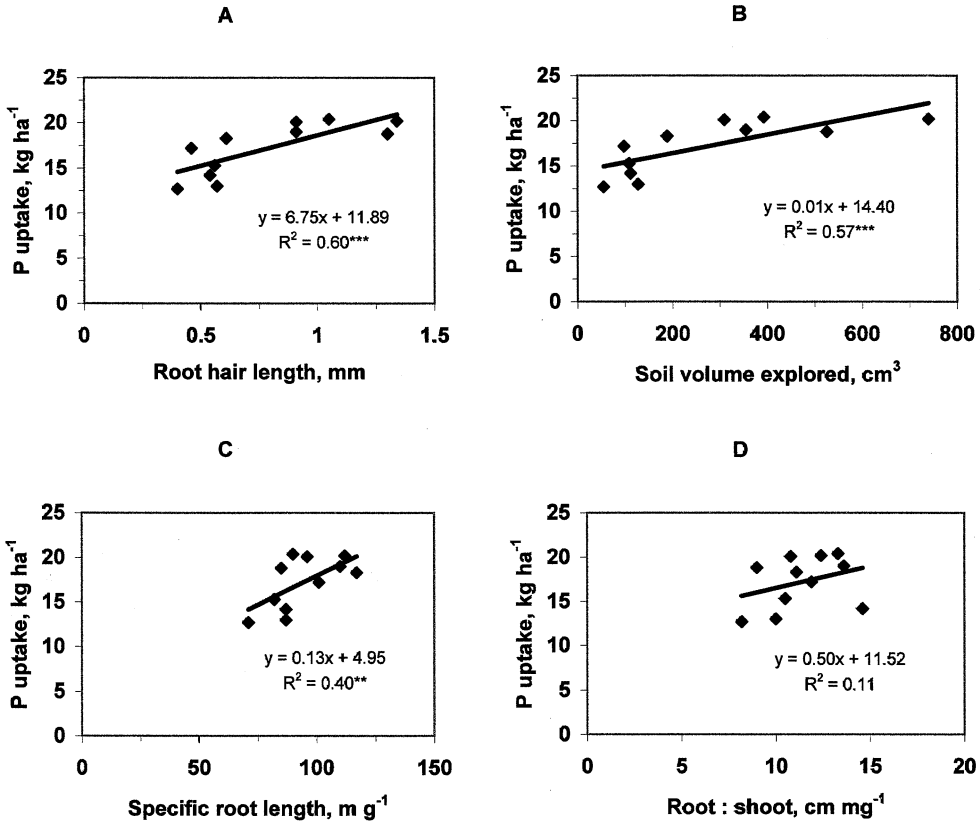

Figure 2. Correlations between root hair length (A), estimated soil volume explored (B), specific root length (C) and root: shoot ratio (D) and phosphorus uptake of barley genotypes in low-P field.

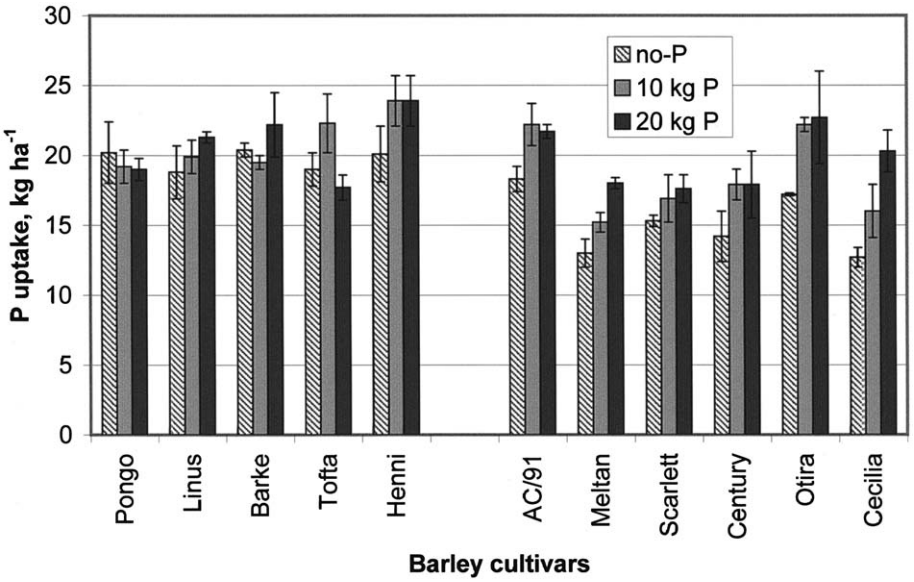

Figure 3. Phosphorus uptake of barley genotypes in the field after 87 days growth period at three levels of P fertilization. (0P = no P since 1966, soil solution P = 3 μM; 10P = 10 kg P ha^{-1} $year^{-1}$, Soil solution P = 6 μM; 20P = 20 kg P ha^{-1} $year^{-1}$; soil solution P = 10 μM). The error bars represent the *LSD* at the 5% level.

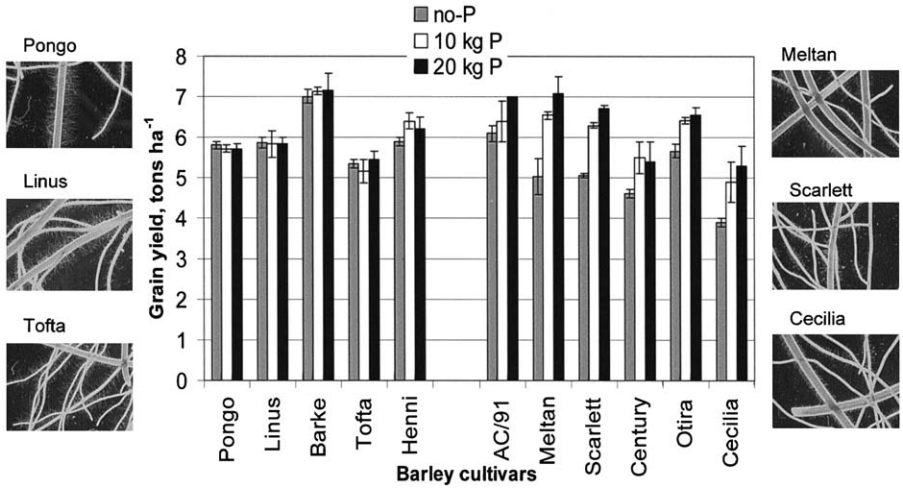

Figure 4. Grain yield at three levels of P fertilization and root hairs of barley genotypes in the field. (0P = no P since 1966, soil solution P = 3 μM; 10P = 10 kg P ha^{-1} year^{-1}, Soil solution P = 6 μM; 20P = 20 kg P ha^{-1} year^{-1}; soil solution P = 10 μM). The error bars represent the *LSD* at the 5% level.

Although grain yield is a rather complex trait, it is interesting to note that root hair length was clearly related to grain yield stability. Root hair length is regulated by P supply and the increase in root surface area through root hairs proliferation in low-P environment is a carbon saving (Hetrick 1991) and efficient strategy for P acquisition (Bates and Lynch, 2000), as revealed by lower cost-benefit ratio of *Arabidopsis* plants with root hairs than the root hair *defective* mutants (*rhd6* and *rhd2*). Hence the barley cultivars possessing long root hairs may acquire P by investing less carbon in more efficient root system and perhaps might be diverting the conserved carbon for grain production. Increase in grain yield has been often observed to occur without an increase in root mass (Smulalski and Oberauf 1990; Greef and Kullmann, 1992). Root hairs, which are often neglected, represent about 2% of the root mass (Clarkson, 1996; Röhm and Werner, 1987) but can enlarge the nutrients and water absorbing root surface area up to three times (Gahoonia et al., 1997). Recent studies also revealed that root hairs not only provide extra root surface area, but they also mediate extra release of organic acids, especially citrate (Narang et al., 2000) and acid phosphatase (Gahoonia et al., 2001) in the rhizosphere. The genotypes with long root hairs as a combination of these processes can be expected to possess the advantage of getting hold of extra P despite low easily soluble P in the soil, which they could translate into grain yield. Given the fact that grain yield is a complex agronomic trait, the observation should be treated with caution. However, the observation is logical, considering the discussed multifarious role of root hairs in synchronized liberation of orthophosphate from both mineral and organic P complexes, following its prompt absorption from the root hair zone.

Variable response of P fertiliser applications to P uptake and grain yield is known (Bolland, 1994; John and Wahbi, 1992; Reuter et al., 1995). The variability has been attributed to unpredictable residual values of P fertilisers, complex genotype-environmental interactions and diverse soil P test methods applied. The results of present study suggested that the knowledge gap in the diversity of root and root hair traits of the cultivated genotypes in the field trials might have added to the frequently reported discrepancies in P response to grain yields. In the present study the P response to grain yield could be observed for genotypes with short root hairs, but not for those with long root hairs (Figure 4). The barley genotypes with long root hairs may not substitute P fertilisation entirely, but will be of added advantage for enhancing the efficiency of P fertilisation and for sustaining high yields in low P soils.

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