Plant and Soil **211:** 269–281, 1999.

Phosphorus (P) acquisition of cereal cultivars in the field at three levels of P fertilization

Tara S. Gahoonia[1,*], Niels E. Nielsen[2] and Ole B. Lyshede[3]
The Royal Veterinary and Agricultural University,
[1,2]*Department of Agricultural Sciences, Plant Nutrition and Soil Fertility Laboratory, Thorvalsensvej 40, DK-1871 Frederiksberg C, Copenhagen, Denmark;* [3]*Department of Plant Biology, Laboratory of Plant Physiology and Anatomy, Thorvalsensvej 40, DK-1871 Frederiksberg C, Copenhagen, Denmark*

Received 16 December 1998. Accepted in revised form 9 July 1999

Key words: barley, genetic variation, phosphate uptake, rhizosphere, root hairs, wheat

Abstract

Low phosphorus (P) availability in soils and diminishing P reserves emphasize the need to create plants that are more efficient P users. Knowledge of P efficient germplasm among the existing cereal varieties may serve as the basis for improving soil P use by selection and breeding. We had identified some cereal cultivars (winter wheat: Kosack and Kraka; winter barley: Hamu and Angora; spring barley: Canut, Alexis, Salka, Zita;) which differed ($p<0.05$) in P depletion from thin slices (0.2 mm) of the rhizosphere soil under controlled conditions. In the present study, the same cultivars were studied under field conditions at three levels of P supply (no-P, 10 and 20 kg P ha^{-1}) and the differences in P uptake as found in the previous work were confirmed. Under both conditions, the variation between the cultivars was greatest in soil without P fertilizers (no-P) for about 30 years. The variation in P uptake with most cultivars disappeared when 10 kg P ha^{-1} was applied. Root development did not differ between the cultivars much, but there was wide, consistent variation in their root hairs, regardless of growth media (solution, soil column and field). Increase in soil P level reduced the length of root hairs. The variation in root hairs between the cultivars was largest in no-P soil. When 10 kg P ha^{-1} was applied, the root hair lengths did not differ between the cultivars. Barley cultivars with longer root hairs depleted more P from the rhizosphere soil and also absorbed more P in the field. The relationship between root hairs and phosphorus uptake of the wheat cultivars was less clear. The wide variation in P uptake among the barley cultivars in the field and its relationship to the root hair development confirms that root hair length may be a suitable plant characteristic to use as criterion for selecting barley cultivars for P efficiency, especially in low-P soils.

Introduction

Phosphorus (P) is one of the most universal deficient nutrients in soils, hence phosphorus fertilisation is a common practice necessary for good crop production. A major portion of P fertilizers is applied to cereals (Clark, 1990) partly because modern varieties require high P fertiliser applications to maintain high productivity. Concerns are being expressed that due to the limited P resources, lasting only a few more decades, lack of P fertilizers may become a serious problem in the future (Mucchal et al., 1996). To some extent, the problem of limited P resources can be helped through better P cycling in agricultural production systems. But due to decreasing soil P availability with reduced P inputs, rising fertiliser prices, increased ecological awareness of the public leading to tighter legislation of fertiliser use, it is increasingly desirable to produce more with less P in soils. Among strategies for achieving this, the possibility of selecting and breeding of P efficient cereal varieties has been stimulated by the increased knowledge about P uptake differences between crop plants and their cultivars. The differences in P uptake among species

* FAX No: +45 35283460. E-mail: TSG@KVL.DK

or cultivars will hopefully help to reduce costs of P fertilisation and enhance plant productivity with more P efficient plants. A criterion for succeeding in crop improvement/breeding programs for mineral nutrition characteristics is that sufficient variability exists and it is identified for the desired characteristic so that improvement through plant breeding can take place. Evaluation of P efficient germplasm among the existing varieties can serve as the basis for improvement of soil P use by selection and breeding. We had identified some cereal cultivars, which differed in P uptake from rhizosphere soil at three P levels under controlled conditions (Gahoonia and Nielsen, 1996). The differences in P uptake between the cultivars were related to the variation in their root hair length (Gahoonia et al., 1997). The studies under controlled rhizosphere and nutrition conditions allowed minimisation of the non-genetic variation. However, it remained unclear how the cultivars will perform under field conditions. To find an answer to this question, a field experiment was carried out with same cultivars at three levels of P supply. To get more detailed information about the root hair development, two additional experiments were carried out under more controlled conditions, the one with nutrient solution and the other with columns filled with soil originating from the field experiment. This paper reports the observed genetic variation in P uptake of cereal cultivars in the field at three levels of P supply.

Materials and methods

Field experiment

Experimental design

A complete randomised design with 2 replicates was used. 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 was included for assessing the expression of genetic variation between the cultivars with fertiliser applications close to that of 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.

Table 1. Overview of the cereal cultivars studied in the field experiment and their parental germplasm

Winter wheat (*Triticum aestivum* L.)	
Kosack	(Mironovskaja 808 Starke M) Holme M
Kraka	Kranich ×Caribo
Winter barley (*Hordeum vulgare* L.)	
Angora	Breun Stamm 301 a ×Wheinst. W 5907
Hamu	Mammut × Hasso
Spring barley (*Hordeum vulgare* L.)	
Alexis	Breun St. 1622d × Triumph
Canut	Triumph × Magnum
Salka	Elbo × Vada
Zita	Vada × 203/7748

The soil for laboratory studies was sampled to a depth of 20 cm at the sowing time. For studying the effect of soil P supply on length of root hairs, the soil from the field plots 0P, 10P and 20P was used.

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; 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 = 3μM. *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.

Soil phosphorus was extracted with 0.5 *M* $NaHCO_3$ (pH 8.5) (Olsen and Sommers 1982) and P in the extract was analyzed colorimetrically (Murphy and Riley, 1962). Soil solution was obtained by displacement (Adams, 1974)

Sampling of plant material

Aerial parts (DM) from 1 m^2 per plot were harvested 5-6 times during the growth period after 24, 36, (52), 66, 84 and 94 days after germination.

Cultivars

The cereal cultivars (Table 1) for the field experiment were chosen, because in previous work (Gahoonia et al., 1997), they differed most in P uptake from rhizosphere soil under controlled conditions. The spring barley cultivars were grouped into sets of Salka-Zita and Canut-Alexis, because of one common parent. Due to the shortage of seeds of old variety Salka,

the set Salka-Zita could be tested only at 0P and 10P levels.

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 was digested in a mixture of H_2SO_4, H_2O_2 and HNO_3. P was determined colorimetrically (Murphy and Riley, 1962). Phosphorus uptake was calculated from shoot dry weight and P concentration.

Root hair determination

For spring barley cultivars (Salka and Zita) growing in the field, soil cores with intact plants and roots were taken up to about 10 cm soil depth (3 replicates, 25 d 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 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. Ten root hairs were randomly selected and measured on each root segment. The length and density of root hairs of all the root segments were averaged. No mycorrhizal hyphae were seen on roots, when stained with trypan blue.

Nutrient solution experiment

The concern about holes in the small field plots put a constraint on sampling of soil cores for root measurements in the field. Therefore, the ability of the cultivars to produce roots was determined in nutrient solution culture.

Plant growth

To measure roots and root hairs in a nutrient solution culture, the plants (three replicates) were grown in 5-l pots using the nutrient solution (Bc) in Table 2. Its electric conductivity was maintained at 0.63 mS cm^{-1} by addition of maintenance solution (Mt in Table 2) according to a pre-determined relationship between volume added and electric conductivity. 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 was close to that of the soil (pH 5.6) used in the soil columns and 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 d old, six randomly selected root segments (about 5 cm long) from each replicate were placed in a film of water in petri dishes. Root hairs were measured using image analysis as described above. 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).

Soil column experiment

Plant growth

The plants (three replicates) were pre-grown in PVC tube (length 10 cm, diameter 4.4 cm) as described by Gahoonia and Nielsen (1991). Two ceramic fibre wicks were placed along the inner sides and the tube was filled with vermiculite and pre-germinated seeds of the cultivars were transferred. The purposed of the wicks was to supply plants with a nutrient solution. About 12 d after germination, root mats developed at the bottom of the tube, because it was closed by nylon cloth impervious to roots. Then the tube along with the plants was transferred to soil columns, filled into another PVC tube (length 3 cm, diameter 5.6 cm), to the upper side of which; a nylon screen of mesh size 53 μm was glued. Another similar tubes were glued over it and filled with 1-cm soil layer above the screen. Six holes (ca. 1 mm) were made at different places in the nylon screen. The roots first grew into the 1-cm soil layer and then about six roots penetrated the holes and grew into the soil columns. The pre-developed root mats facilitated quick and uniform penetration of roots of similar age through the six holes. The supply of the maintenance solution (Mt in Table 2) via the two wicks was maintained at 20 cm water tension. The uptake of the nutrient solution via the wicks is induced by transpiration. The soil columns (bulk density 1.3 g cm^{-3}) and the 1-cm soil layer were maintained at defined moisture (θ = 0.21) by placing them over small cup-shaped sand baths each fitted with a wick dipping into a reservoir of distilled water.

Table 2. The composition and concentration of Basic (Bc) and maintenance (Mt) solutions

	mM								μM						
Nutrients	NO_3	NH_4	P	S	K	Ca	Mg	Cl	Na	Fe	Mn	Zn	Cu	B	Mo
Bc	5.0	0.0	0.05	0.44	0.58	1.92	0.78	0.10	0.001	50	7.0	0.7	0.7	2.0	0.7
Mt	13	3.2	0.54	0.61	7.16	1.40	0.35	0.40	0.24	15	12	6.0	0.9	4.6	0.2

Root hair determination

After 7 d, the root mats were separated from the soil columns at the interface with a sharp knife, without disturbing the penetrating roots. (If more than 7 d passed, many roots would penetrate through the same hole making it difficult to wash them out of soil and separate them without damaging root hairs). The soil columns were immersed in water overnight in dark at 5 °C. Root hairs and root parameters were measured using image analysis (as described above) on all the roots washed out of the soil columns as described above. 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, relative humidity 75%). More details of the plant growing technique are given in Gahoonia and Nielsen (1991, 1997).

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

Results

Both barley and wheat cultivars differed in their ability to absorb phosphorus and to produce shoot dry matter (DM) in the field. In general, the genetic variation in P uptake and DM production was wider in plots without P application for 30 years and it became gradually less in higher P plots. The variation in P uptake (Figure 1A–C) and DM production (Figure 1D–F) between the winter wheat cultivars Kosack and Kraka disappeared when 20 kg P together with 120 kg N and 120 kg K ha^{-1} was applied. The winter barley cultivars Hamu absorbed more P (Figure 2A–C) and produced more DM (Figure 2D–F) than Angora at 0P and 10P. At 20P level the variation disappeared. Spring barley cultivars, Canut and Alexis differed in P absorption (Figure 3A–C) and DM production (Figure 3D–F). At 0P level Canut was superior to Alexis (Figure 3D), at 10P there was no variation (Figure 3E). At higher P levels (20 kg P) Alexis produced more DM than Canut (Figure 3F), which is in agreement with the performance of Alexis in many agriculture soils, when high fertiliser inputs are applied. These results show that some cultivars performing better under high-input conditions may not perform similar in low-input conditions. Salka absorbed more P (Figure 4A) and produced more DM (Figure 4C) than Zita at 0P level. However, when 10 kg P ha^{-1} was applied, the both cultivars absorbed nearly the same amounts of P and produced similar amounts of DM.

Application of 10 kg P ha^{-1} increased DM of all the cultivars. However, in many cases, the magnitude of such increase was nearly equal to the variation between the cultivars in 0P plots. For example, the amount of DM produced by Zita at 10P is nearly equal to that of Salka in the 0P plot.

There was wide variation in root hair formation of the cultivars regardless of growth media (Figure 5A–5F)). The average root hair length with all the cultivars was slightly longer in the soil culture and field experiment than in nutrient solution. The root hair density appeared to be lower in soil than in solution (Table 3), though; the differences were not significant ($p<0.05$). Root hairs from solution culture were nicely arranged perpendicular to the root surface (Figure 5A–5B) and it was easier to measure their actual length and density. The root hairs washed out of soil-based systems (Figure 5C–5F) were curled, probably because of their growth in soil pores. This made it difficult to determine their precise length and density with image analysis. We measured only the extension of root hair zone and estimated their number on the roots. Therefore, it may be so that the actual lengths of root hairs in soil culture and in the field are slightly greater. However, the extent of variation in root hairs of the cultivars remained almost the same, regardless of the plant culture technique applied. These results indicate that genetic variation in root hairs can be assessed with reasonable accuracy in nutrient solution culture.

The variation between the root hairs of the cereal cultivars was significant. For example in soil, the root hair length of spring barley cultivar Salka was

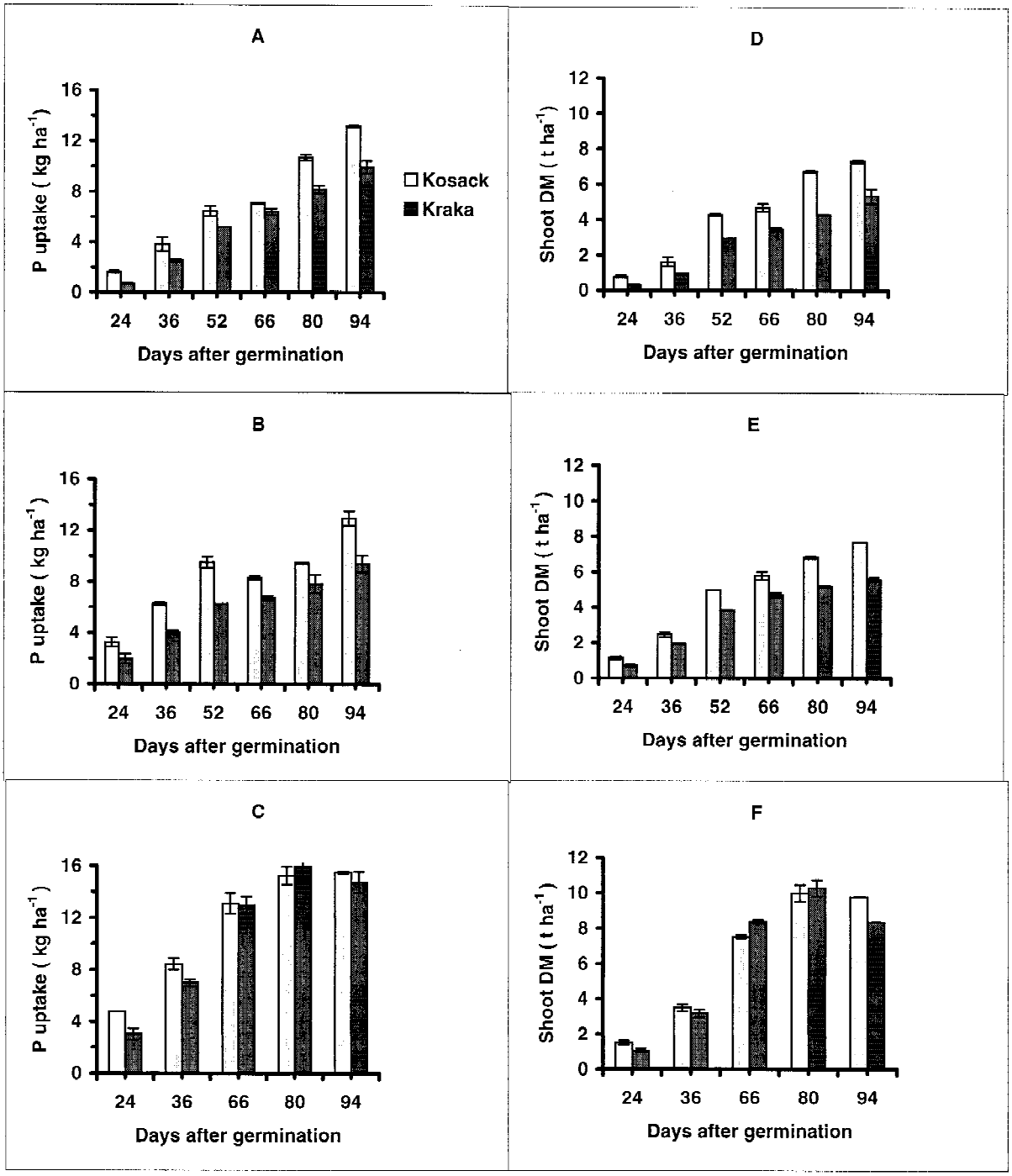

Figure 1. Phosphorus (P) uptake of winter wheat cultivars Kraka and Kosack in the field without P fertiliser since 1966 (A), with 10 kg P ha^{-1} (B), with 20 kg P ha^{-1} (C) and the corresponding shoot dry weight (D, E, F).

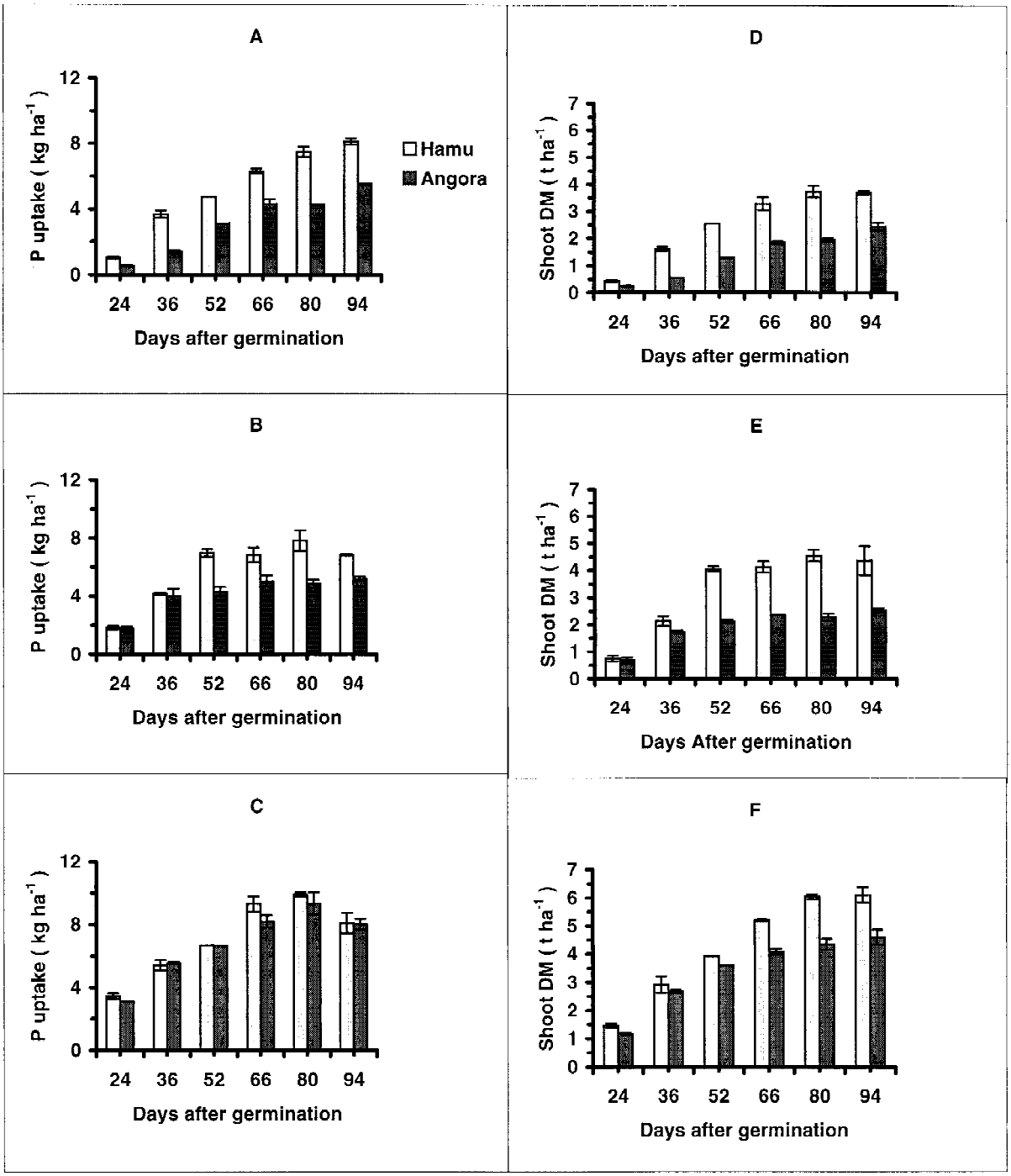

Figure 2. Phosphorus (P) uptake of winter barley cultivars Hamu and Angora in the field without P fertiliser since 1966 (A), with 10 kg P ha^{-1} (B), with 20 kg P ha^{-1} (C) and the corresponding shoot dry weight (D, E, F).

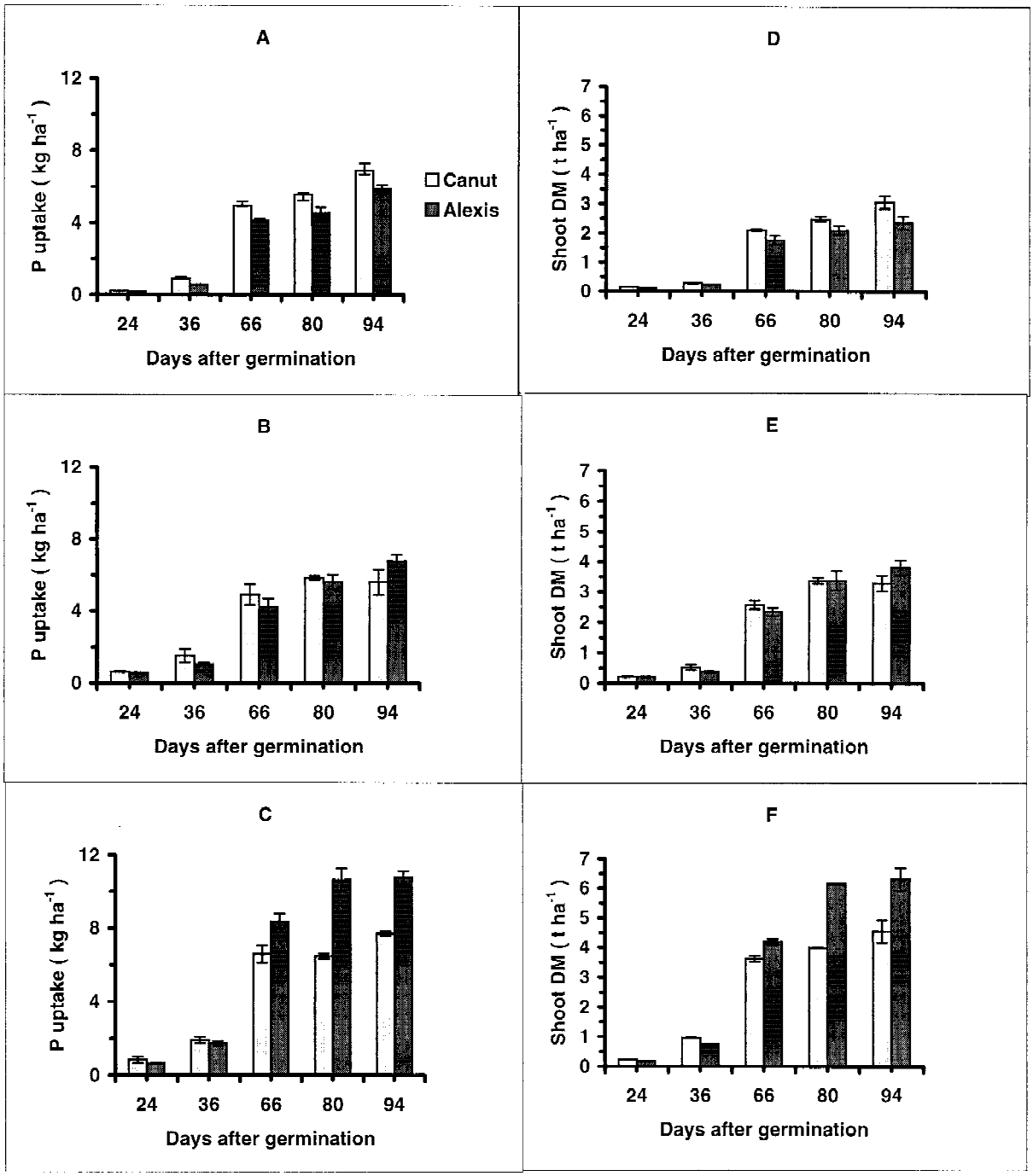

Figure 3. Phosphorus (P) uptake of spring barley cultivars Canut and Alexis in the field without P fertiliser since 1966 (A), with 10 kg P ha^{-1} (B), with 20 kg P ha^{-1} (C) and the corresponding shoot dry weight (D, E, F).

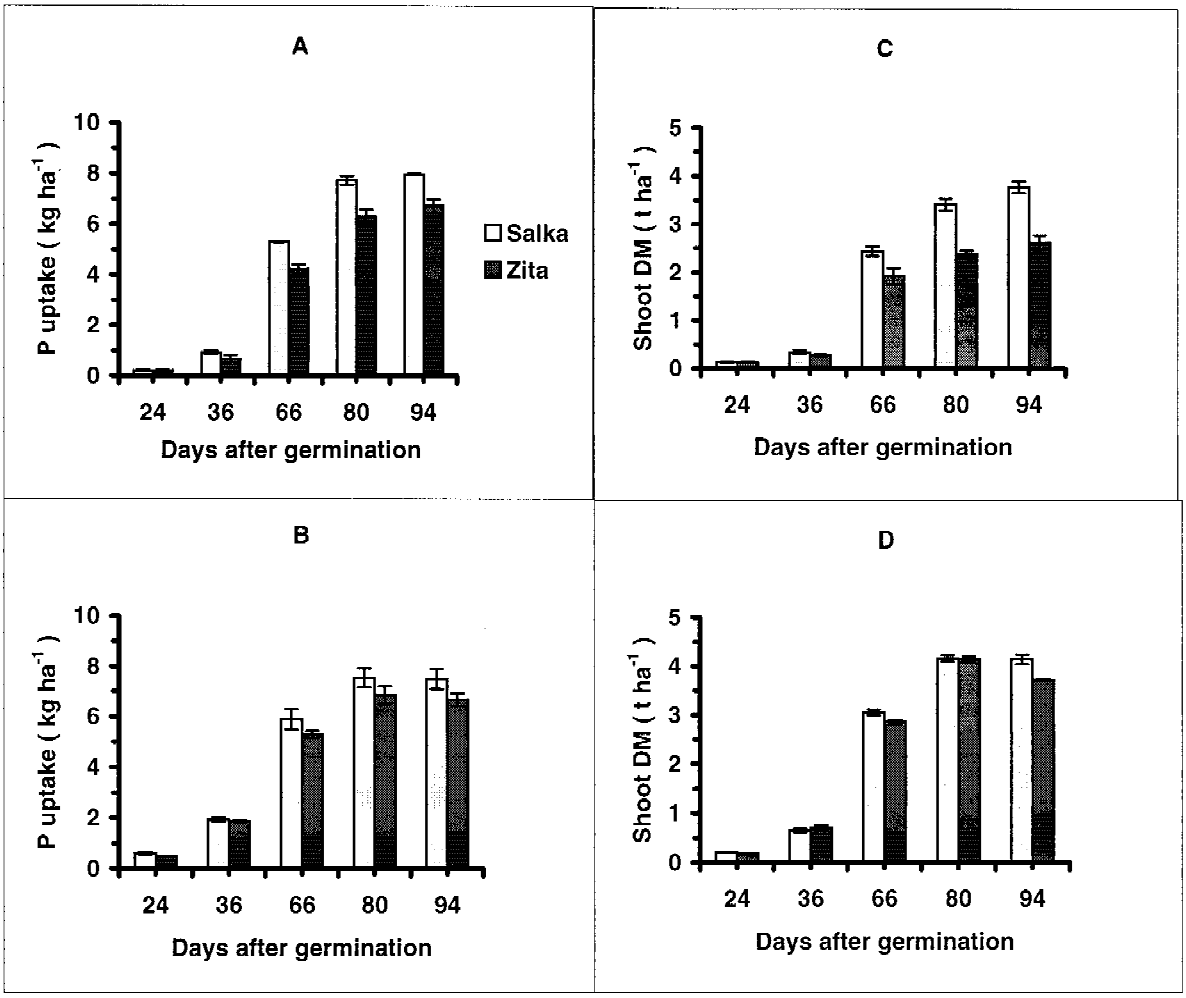

Figure 4. Phosphorus (P) uptake of spring barley cultivars Salka and Zita in the field without P fertiliser since 1966 (A), with 10 kg P ha^{-1} (B), with 20 kg P ha^{-1} (C) and the corresponding shoot dry weight (D, E, F).

1.75 times greater than that of Zita (Table 3). Salka had 1.6 times denser root hairs as compared to Zita. Winter barley cultivar Hamu had 1.9 times longer and 1.4 times denser root hairs than Angora. Root hairs of winter wheat cultivar Kraka were much longer (1.26±0.17 mm) and denser (41±5 hairs mm^{-1} root) than those of Kosack which had shorter (0.59±0.16 mm) and fewer (19±4 hairs mm^{-1} root) root hairs in soil culture (Table 3).

The winter wheat cultivar Kraka produced more root length than Kosack (Figure 6A). Winter barley cultivar Angora produced more roots than Hamu. The difference in specific root lengths (root fineness expressed as m g^{-1} dry root weight) of spring barley cultivars Salka-Zita and Canut-Alexis was not significant ($p>0.05$). The specific root hair length (*average root hair length* × *number of root hairs* mm^{-1} *root*) of Kraka was nearly five times greater than that of Kosack (Figure 6B). Hamu had nearly three times greater total root hair length than Angora. The total root hair length of Canut was two times greater to Alexis and that of Salka was nearly 3 times greater to Zita. The variation in specific root length (Figure 6A) did not explain the observed variation in P uptake of the cultivars. All the barley cultivars with longer and denser root hairs absorbed more P, especially in low-P soil. The variation in root hair length between the cultivars was largest in soil (0P) where no P was applied since 1966. Increase in P level reduced the length of root hairs and the variation between the cultivars was also reduced (Figure 7). For example, when 10 kg P ha^{-1}

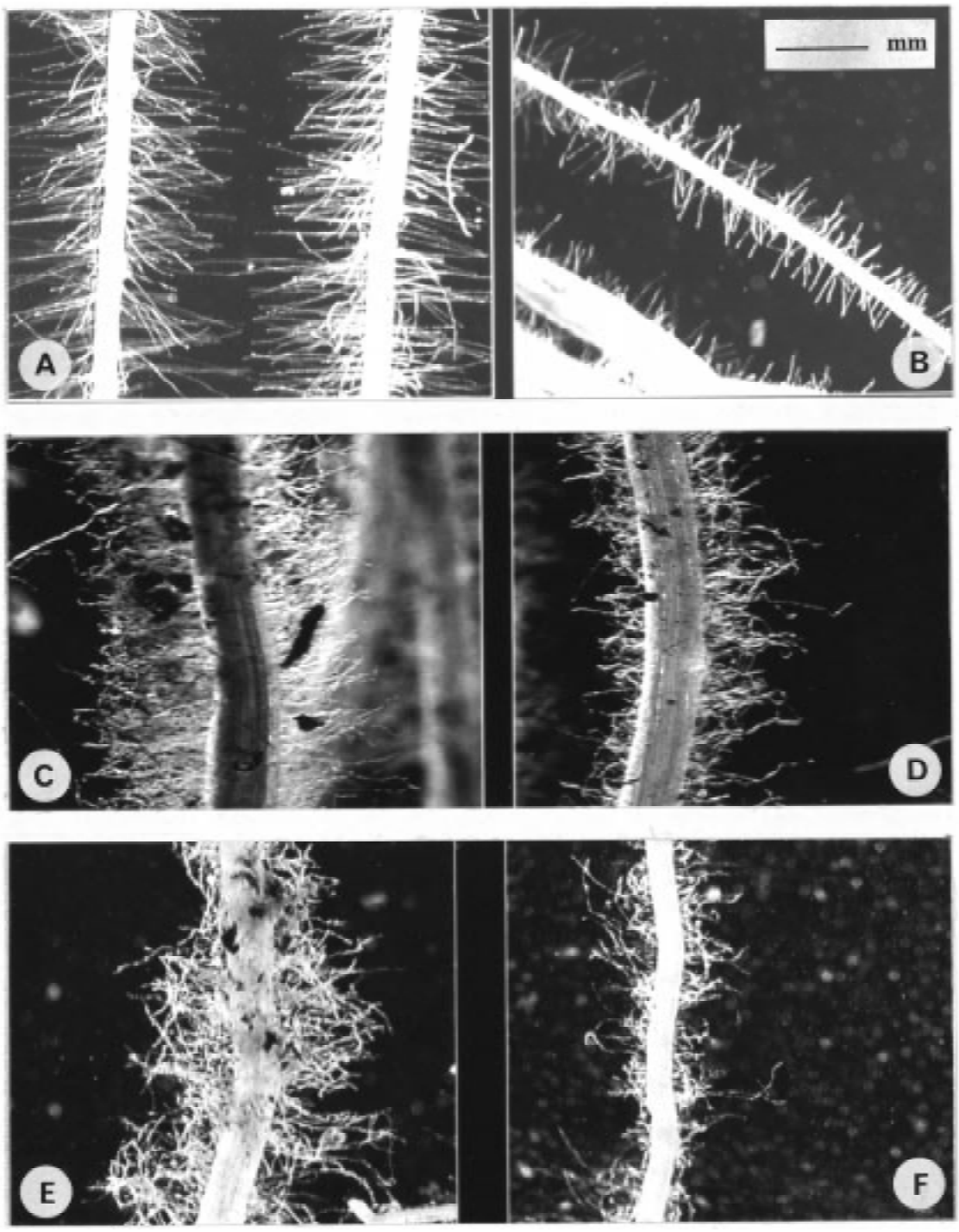

Figure 5. Root hairs of two spring barley cultivars (Salka and Zita) in different plant culture techniques. (A) Salka and (B) Zita in nutrient solution culture. (C) Salka and (D) Zita in soil culture. (E) Salka and (F) Zita in field experiment.

Table 3. Length and density of root hairs on roots of barley and wheat cultivars grown in nutrient solution, soil and field. (mean±stdv., n = 180)

	Barley cultivars				Wheat cultivars	
	Salka	Zita	Hamu	Angora	Kraka	Kosack
Root hair length (mm)						
In nutrient solution	1.02 ±0.22	0.54 ±0.16	1.10 ±0.30	0.52 ±0.20	1.27 ±0.26	0.49 ±0.24
In soil	1.10 ±0.16	0.63 ±0.18	1.07 ±0.27	0.57 ±0.14	1.26 ±0.17	0.59 ±0.16
In field	1.14 ±0.20	0.62±0.14				
Root hair density (number mm^{-1} root)						
In nutrient solution	32 ±4	21 ±3	30±2	27 ±2	38 ±3	24 ±3
In soil	30 ±6	18	±428 ±3	20 ±4	41 ±5	19 ±4
In field	28 ±6	20 ±4				
Root diameter (mm)						
In nutrient solution	0.20 ±0.05	0.17 ±0.06	0.17 ±0.03	0.15 ±0.04	0.17 ±0.04	0.15 ±0.03

was applied, the length of root hairs of spring barley cultivars Salka and Zita was nearly equal.

Discussion

The cereal cultivars differed in P uptake and DM production in the field. The variation between the cultivars was highest in plots without P fertilizer (0P). The wide variation in P uptake between the existing cereal cultivars in low P soil indicates that unconscious selection for P efficiency has occurred. It may serve as basis for further improvement of P efficiency of cereals. The differences in P uptake between the barley cultivars, especially in low P soil, were closely related to their root hair formation. The variation in P uptake and root hairs became gradually less when 10 and 20 kg P ha^{-1} was applied, because increasing P levels had negative effect on root hair formation (Figure 7) and at higher P levels the variation in root hairs decreased. The observed P uptake of all the barley cultivars in the field in the present field study corresponded to their ability to acquire P from their rhizosphere soil as observed in previous laboratory studies (Gahoonia et al., 1997). Hence the results obtained with the barley cultivars using the laboratory methods (Gahoonia and Nielsen, 1991, 1992) to study P uptake from rhizosphere soil agreed well with the field study.

With winter wheat cultivars, the relationship between root hairs and P uptake was less clear. Therefore, other factors seem to be involved. Under the field conditions winter wheat cultivar Kosack was superior to Kraka, despite better root development and longer and denser root hairs of Kraka. This is not in agreement with the results of previous rhizosphere studies with wheat cultivars (Gahoonia and Nielsen, 1996). In the rhizosphere studies, soil P concentration in the immediate root vicinity of Kosack was lower (0.48 μmole cm^{-3}) than Kraka (0.60 μmole cm^{-3}). Therefore, it appears that winter wheat cultivar Kosack in the field has higher root exudation for releasing bound soil P. Kosack may possess the greater ability to absorb P from lower soil solution P concentration i.e. its C_{min} (lowest effective minimum concentration) is lower than Kraka (Nielsen and Schjørring, 1983).

The role of root development in P uptake by cereal cultivars has been subject of many investigations (Römer et al., 1987). But the role of root hairs is often neglected for assessing the role of root parameters in genetic variation in phosphorus uptake. The results of this study show that root hairs are very important factor in causing the variation in P uptake of barley cultivars in the field. The direct evidence on role of root hairs in P uptake from soil (Gahoonia and Nielsen, 1998) is further strengthening of this view. With conventional fertilisers inputs (20P), root hair formation was reduced and the variation between

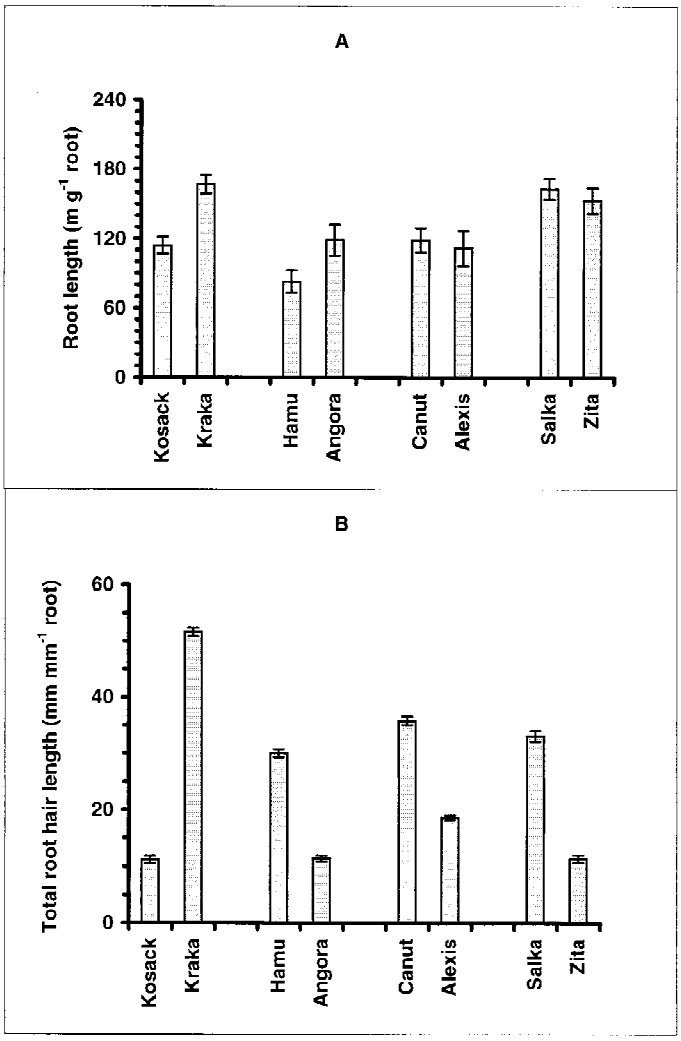

Figure 6. Root length (A) and total root hair length (B) of the cereal cultivars.

the cultivars was narrowed (Figure 7). Therefore, it seems that in conventional agriculture, the ability of root hairs to increase root surface area and P uptake is decreased by addition of fertilisers. Root hairs are the visible component of root-soil interface. This may offer the possibility of quick screening of larger number of cereal lines for variation in root hairs and further dissection of genetic control of root hair formation (Schiefelbein and Somerville, 1990).

Application of 10 kg P ha^{-1} increased shoot biomass (DM) of the cultivars. However, the increase was nearly equal to the difference between the cultivars in low P soil (0P plots). The amount of DM produced by Zita in 10P plot was nearly equal to those of Salka in 0P plot. The case was similar with Alexis in 10 P and Canut in 0P plot. Thus, in low P soil, the P efficient barley cultivars seem to produce same amount of DM with 10 kg ha^{-1} less P fertiliser application. These results indicate the added advantage of selection and breeding for P efficiency for maintaining productivity in low P soils. In our studies we did not observe the presence of mycorrhizal hyphae in soil column and in field experiment, probably because of short time periods after which roots were sampled for the root hair studies. Root hair formation and mycorrhiza may be considered two complimentary processes for acquisition of diffusion limited soil nutrients such as phosphorus. As compared to root hair formation (Clarkson, 1996; Röhm and Werner, 1987), mycorrhizal colonisation seems

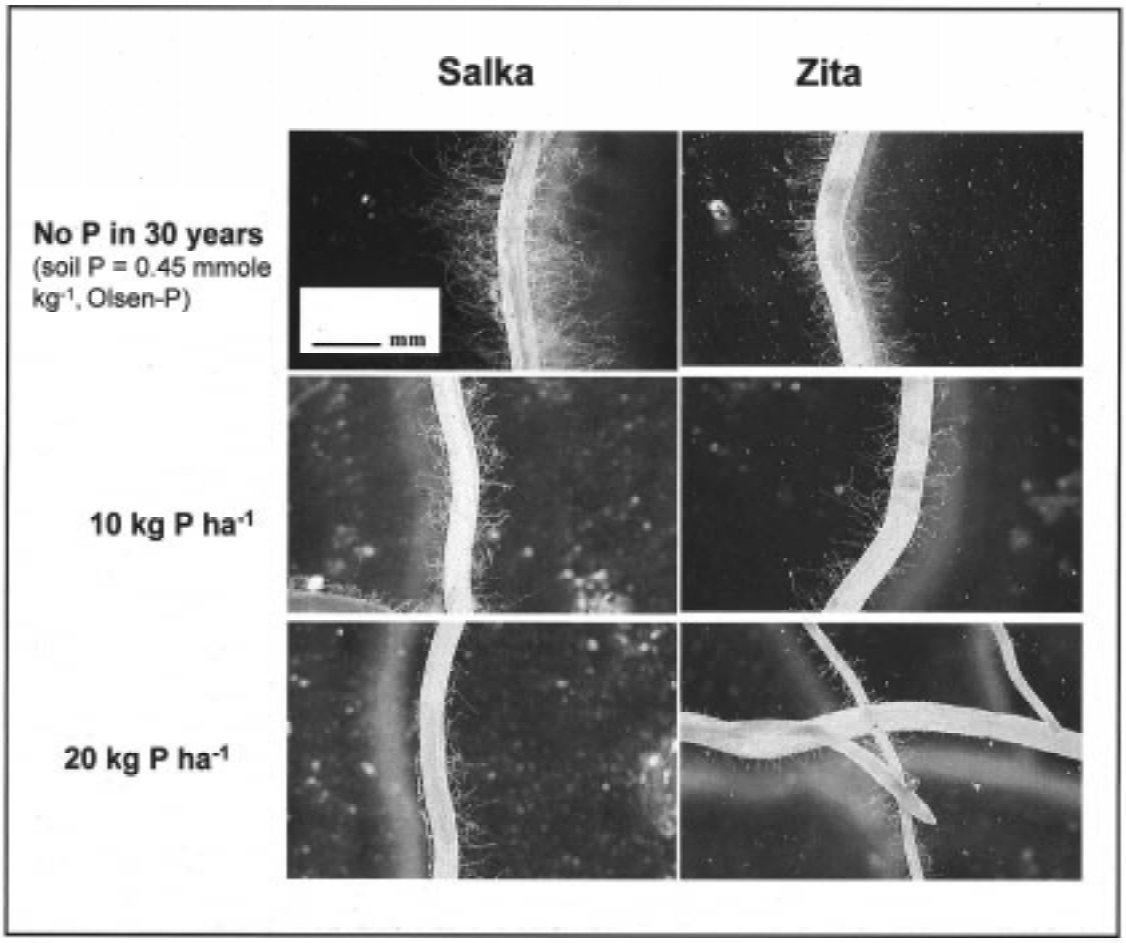

Figure 7. Effect of phosphorus fertilisation on root hairs of spring barley cultivars Salka and Zita.

to represent a significantly higher photosynthetic carbon cost (Jakobsen, 1991). The variation in degree of VAM colonisation between 27 wheat lines (Kapulnik and Kushnir, 1991) and between 10 barley cultivars (Jakobsen and Nielsen, 1983) was not significant. This suggests that even though the occurrence of mycorrhizas in agro-ecosystems is quite universal, its variation and beneficial effect for P acquisition may be less for cereals with extensive root systems having long root hairs (Schweiger et al., 1995).

Root hairs develop very soon after germination. Significant mycorrhizal development occurs only after 3–6 weeks (Baon et al., 1994; Jakobsen et al., 1992). In annual crops like cereals, nearly whole P uptake from soil occurs in the first 10 weeks. The difference in time required for significant mycorrhizal development and root hair formation also suggests that the significance of root hairs in P acquisition may be much greater in cereals, thus helping them to absorb large part of P in early growth phases.

Conclusions

Both previous laboratory (Gahoonia et al., 1997) and the field studies confirmed that the available cereal cultivars differ considerably in P uptake, showing that unconscious selection for P efficiency has occurred. It provides a basis for upgrading P efficiency by targeted selection and breeding. The variation in P uptake among the cultivars was largest in the plot, where P fertilisation was withheld for about 30 years (Olsen P content = 0.45 mmole P kg^{-1} soil), suggesting that we can make best use of genetic variation in low P soils. With increasing levels of P fertilisation, the variation gradually disappeared, showing that in high-

input conventional agriculture, we do not make use of the genetic variation in P uptake between cereal cultivars. With barley cultivars the variation in P uptake was clearly due to the variation in the root hair formation, which was consistent, regardless whether the cultivars were grown in nutrient solution culture, pots or in the field. Therefore, it seems possible to screen large number of cereal cultivars using nutrient solution. The results of this study suggest that root hairs would be a suitable plant parameter for selecting P efficient barley cultivars.

Acknowledgement

The financial support for this research work was provided by The Danish Veterinary and Agricultural Research Council. We thank Birthe K Nielsen for laboratory assistance and Keld Skov Nielsen for help in field experiment.

References

Adams F 1974 Soil Solution. *In* The Plant root and its Environment. Ed. EW Carson. University press, Virginia, Charlottesville, USA.

Baon J B, Smith S E and Alston A M 1994 Growth response and phosphorus uptake of rye with long and short root hairs: Interactions with mycorrhizalinfections. Plant Soil 167, 247–254.

Clark R B 1990 Physiology of cereals for mineral nutrient uptake, use and efficiency. *In* Crops as Enhancers of Nutrient Use. Eds VC Baligar and RR Duncan. pp. 131–183. Academic Press Inc.

Clarkson D T 1996 Root structure and sites of ion uptake. *In* Plant Roots: The Hidden Half. Eds Y Waisel, A Eshel and U Kafkaki. pp 483–510. Marcel Dekker, Inc. New York, Basel, Hongkong.

Ewens M and Leigh R 1985 The effect of nutrient solution composition on the length of root hairs of wheat. J. Exp. Bot. 36 (106), 713–742.

Gahoonia T S and Nielsen N E 1991 A method to study rhizosphere processes in thinsoil layers of different proximity to roots. Plant Soil 135, 143–146.

Gahoonia T S and Nielsen NE 1992 Control of pH at soil-root interface. Plant Soil 140, 49–54.

Gahoonia T S and Nielsen N E 1996 Variation in acquisition of soil phosphorus among wheat and barley genotypes. Plant Soil 178, 223–230.

Gahoonia T S, Care D and Nielsen N E 1997 Root hairs and acquisition of phosphorus by wheat and barley cultivars. Plant Soil 191, 181–188.

Gahoonia T S and Nielsen N E 1997 Variation in root hairs of barley cultivars doubled phosphorus uptake from soil. Euphytica 98 (3), 177–182.

Gahoonia T S and Nielsen N E 1998 Direct evidence on participation of root hairs in Phosphorus (^{32}P) uptake from soil. Plant Soil 198, 147–152.

Jakobsen I and Nielsen N E 1983 Vesicular Arbuscular Mycorrhiza in field-grown crops. I. Mycorrhizal infection in cereals and peas at various time and soil depths. New Phytol. 93, 401– 413.

Jakobsen I 1991 Carbon metabolisms in mycorrhiza. *In*: Methods in Microbiology. Eds JR Norris, DJ Read and AK Varma Vol. 23, pp 149–180.

Jakobsen I, Abbott L K and Robson A D 1992 External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum.* I. Spread of hyphae and phosphorus inflow into roots. New Phytol. 120, 371–380.

Kapulnik Y and Kushnir U 1991 Growth dependency of wild, primitive and modern cultivated wheat lines on vesicular-arbuscular mycorrhiza fungi. Euphytica 56, 27–36.

Murphy J and Riley J P 1962 A modified single solution method for determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.

Muchhal U S, Padro J M and Raghothama K G 1996 Phosphate transporters from higher plant *Arabidopsis thaliana*. Proc. Natl. Acad. Sci. USA, Vol. 93, 10519–10523.

Nielsen N E and Schjørring J K 1983. Efficiency and kinetics of phosphorus uptake from soil by barley genotypes. Plant Soil 72: 225–230.

Olsen S R and Sommers L E 1982 Phosphorus. In: Methods of soil analysis, Part 2, Chemical and Microbiological properties. ASA-SSSA, 677 S. Segoe Rd. Madison, USA.

Röhm M and Werner D 1987 Isolation of root hairs from seedlings of *Pisum sativum*. Identification of root hair specific proteins by *in situ* labelling. Physiol. Plant. 69, 129–136.

Römer W J, Augustin J and Schilling G 1988 The relationship between phosphate absorption and root-length in nine wheat cultivars. Plant Soil 111: 199–201.

SAS Institute Inc. 1989 SAS/STAT. User Guide. Version 5. SAS Institute Inc., Cary, NC, USA.

Schiefelbein J W and Somerville C 1990 Genetic control of root hair development in *Arabidopsis thaliana* L. Plant Cell 2, 235–242.

Schweiger P F, Robson A D and Barrow N J 1995 Root hair length determines beneficial effects of a *Glomus* species on shoot growth of some pasture species. New Phytol. 131, 247–254.

Section editor: R J Haynes