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Differential responses of root and root hair traits of spring wheat genotypes to phosphorus deficiency in solution culture

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ABSTRACT

Root plasticity is important for plants to adapt to heterogeneous nutrient environments. The differential responses of six spring wheat genotypes were investigated; the plants had been subjected to deficient (2 µmol) and abundant phosphorus (P) (200 µmol) concentration. Root (length, surface area and diameter) and root hair traits (length and density), soil acidification and uptake of macro- and micronutrients were determined. Under low P supply all genotypes exhibited symptoms of P stress, such as poor shoot and root growth, starch accumulation and a release of substantial quantities of proton and acid from roots. Larger genotypic differences in root hair length and density than root length, surface area and diameter were observed. In response to P stress genotype April Bearded responded strongly by increasing its root hair density, while A35–213 and Hankkijan Tapio substantially increased root hair length. Other genotypes showed less positive responses or even negative ones in root hair traits. Thus, density of root hairs appears to be a more P-regulated and P-responsive trait than root hair length. April Bearded acidified the most and Hindy62 released most organic acid in response to P deficiency.

Keywords: hydroponics; macronutrient; *Triticum aestivum* L.; nutrient accumulation; root vigour

Phosphorus (P) is the macronutrient often limiting plant growth and productivity most due to its low mobility and solubility in soil. Identifying improved crop traits and agronomic soil management measures are strategies to address the problem of suboptimal P nutrition (Veneklaas et al. 2012). Plants show plasticity in root growth, and some crop cultivars possess morphological, anatomical and physiological adaptations to acquire P under low P supply (Lynch 2011). Such cultivars grow more and larger roots, or longer and denser root hairs to increase the exploited soil space and root-soil contact to increase P uptake (Schachtman et al. 1998, Wang et al. 2016). Hence, plants respond to different P conditions by regulating root system structure and root hairs, and these P-regulated root traits can be associated with high P uptake. Superior root and root hair traits are also associated with higher yield potential (Gahoonia and Nielsen 2004), enhanced water uptake and increased drought stress tolerance (Brown et al. 2012).

Therefore, identifying specific P-regulated traits and P-efficient crop varieties is particularly important in anticipation of decreasing non-renewable P resources, which triggers modern plant breeding programs (Manschadi et al. 2014). Analyses in solution culture facilitate measurements on root and root hair traits and root exudation, as they (1) minimize damage to root and root hairs during harvest; (2) exclude interference by spatial and temporal soil heterogeneity; and (3) allow a precise control over P concentration in the growing medium. In addition to root system structure, exudation of organic acids can also facilitate P uptake. Considerable research has been done on root hairs and correlation with P uptake, but the response of root and root hair traits of spring wheat to different P conditions has not been studied, yet. The objective of the present study was thus to as-

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sess the responses of root and root hair traits to P deficiency in different spring wheat genotypes.

MATERIAL AND METHODS

Spring wheat (*Triticum aestivum* L.) was cultivated hydroponically in 4-L light-impermeable polyethylene buckets, with three individual plants in each bucket. Seedlings were germinated on vermiculite and then transferred to hydroponic culture. Plants were grown in a completely randomized design in a climate-controlled glasshouse at the Faculty of Science, University of Copenhagen, Frederiksberg with 18/15°C day/night temperature at a photon flux density of 300 μmol/m/s, under a 16-h day/8-h night cycle. The culture solutions were continually aerated and their pH was maintained between 5.8–6.0 with daily additions of KOH and HCl. All nutrient solutions were replaced every five days. Six spring wheat genotypes with variable root traits were used for the experiment: A35-213, Farah, April Bearded, Hindy62, Hankkijan Tapio and Dacke (Wang et al. 2016). Plants were exposed to deficient (2 μmol/L P) and abundant P concentrations (200 μmol/L P). The basal nutrient solution was composed of 2 μmol/L or 200 μmol/L KH_2PO_4, 0.2 mmol/L K_2SO_4, 0.3 mmol/L $MgSO_4$, 0.1 mmol/L NaCl, 0.3 mmol/L Mg $(NO_3)_2$, 0.9 mmol/L Ca $(NO_3)_2$, 0.6 mmol/L KNO_3, 1 μmol/L $MnCl_2$, 0.8 μmol/L Na_2MoO_4, 0.7 μmol/L $ZnCl_2$, 0.8 μmol/L $CuSO_4$, 2 μmol/L H_2BO_3, 1 μmol/L $NiSO_4$ and 50 μmol/L Fe-EDTA. Each treatment was replicated four times. Plants were harvested 25 days after transplanting. Shoots and roots were rinsed in double deionized water. The roots were stored in 25% v/v ethanol immediately after rinsing.

All root systems were analysed using the WinRHIZO image analysis system (Regents Instruments Inc., Quebec, Canada). Root hairs were measured following the method of Wang et al. (2016). H^+ exudation and total acid exudation rates were determined by the procedures described in Yan et al. (2004) with minor modifications, in which intact roots were incubated in 0.5 mmol/L $CaCl_2$ plus low P (2 μmol/L P) or high P (200 μmol/L P) concentration to collect root-exuded acid for determination of total H^+ exuded, and then total acid in the solution was measured by back titration with 0.1 mol/L NaOH. The dry matter (DM) of shoot and root samples was determined after oven drying to constant weight at 70°C. After grinding, the samples were digested in a microwave oven with HNO_3 and HCl in a 1:3 v:v mixture, then macro- and micronutrient concentrations were measured using inductively coupled plasma-optical emission spectroscopy (ICP-OES) (Optima 5300 DV, Perkin Elmer Inc., Connecticut, USA). Total N was analysed using the Dumas dry combustion method in a system consisting of an ANCA-SL Elemental Analyser coupled to a 20-20 Mass Spectrometer (Sercon Instruments, Crewe, UK).

The data were analysed by analysis of variance (ANOVA) using SAS (SAS Institute, Inc., 2011) at a significant level of 5%. Duncan's multiple range test was applied to assess differences between treatments at a significance level of 5%. Linear regression analyses were used to determine relationships between the measured parameters.

RESULTS

Root and root hair traits. Across the P treatments, April Bearded and Hindy62 produced the significantly highest root length (RL) and root surface area (RSA), whereas A35–213 and Hankkijan Tapio produced the lowest RL and RSA (Figure 1a, b). Root diameter was significantly higher for Farah and Hindy62 (Figure 1c). All the genotypes had a similar response to deficient or abundant P supply. Across the genotypes, plants at the abundant P supply had significantly higher RL, RSA and root diameter than those under the deficient P supply.

Analysis across the P levels showed that April Bearded, Farah, Hindy62 and Dacke had longer root hair length (RHL) than the other genotypes (Figure 2a). For root hair density (RHD) and total length of root hair/mm root (TLRH), April Bearded, Hindy62 and Hankkijan Tapio had denser root hairs and greater TLRH than the other genotypes (Figure 2b,c). Across the genotypes, RHL was similar between the two P supplies. However, RHD and TLRH were significantly higher under the deficient P than the abundant P supply. In response to P limitation April Bearded responded strongly by increasing root hair density (Figure 2b), while A35–213 and Hankkijan Tapio rather increased root hair length (Figure 2a). The other genotypes showed less positive responses or even reductions in these root hair traits.

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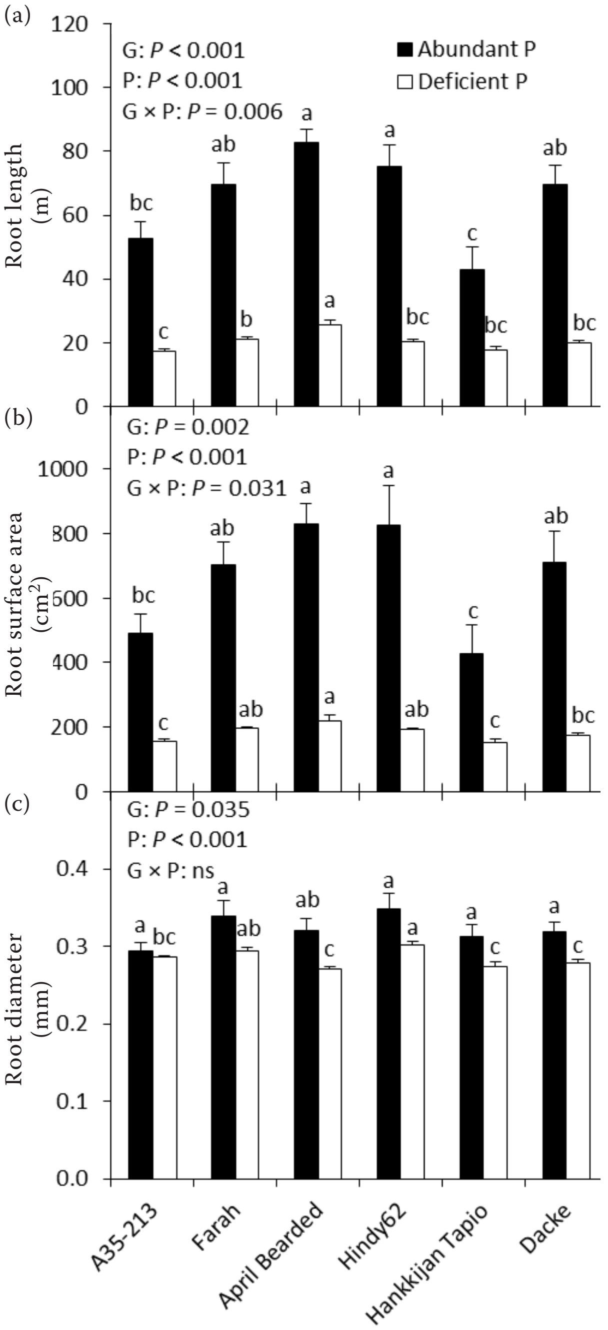

Figure 1. Root length, surface area and diameter of six spring wheat genotypes under abundant and deficient phosphorus (P) supply. Statistical analyses are based on a two-way ANOVA with the factors genotypes (G) and P levels (P) and the interaction between these two factors (G × P). Different letters above columns indicate significant differences among genotypes at the 5% significance level according to the Duncan's multiple range test. ns – not significant. Error bars indicate the standard error of the means ($n = 4$)

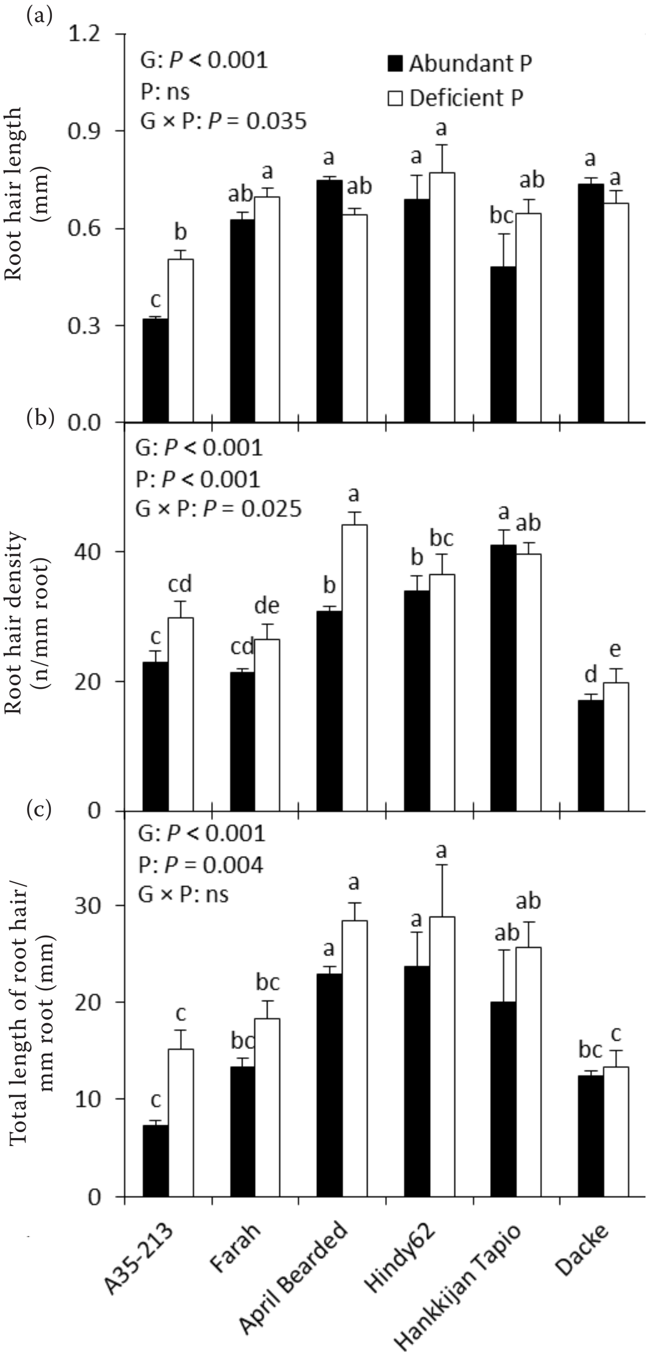

Figure 2. Root hair length, density and total length of root hairs per mm root of six spring wheat genotypes under abundant and deficient phosphorus (P) supply. Statistical analyses are based on a two-way ANOVA with the factors genotypes (G) and P levels (P) and the interaction between these two factors (G × P). Different letters above columns indicate significant difference among genotypes at the 5% significance level according to the Duncan's multiple range test. ns – not significant. Error bars indicate the standard error of the means ($n = 4$)

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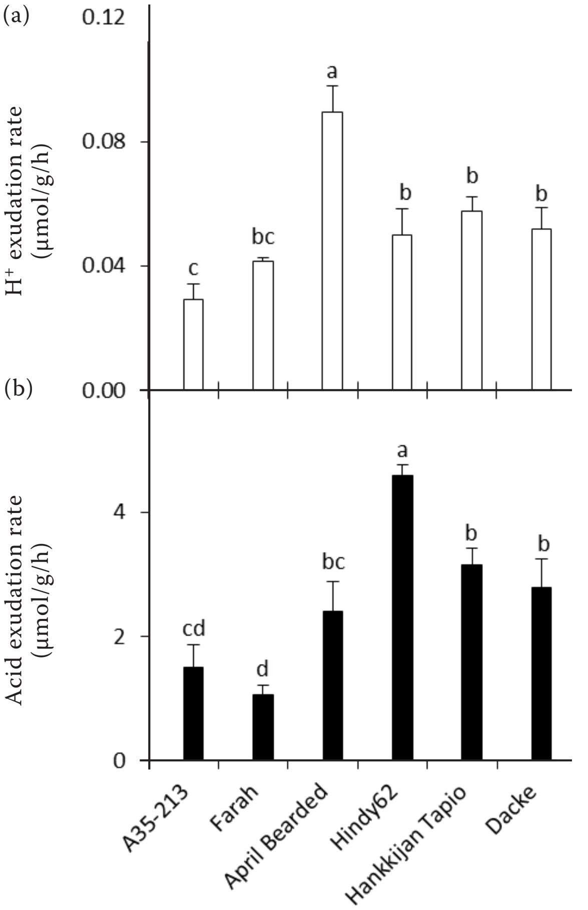

Figure 3. The H$^+$ and organic acid exudation rate of roots of six spring wheat genotypes under phosphorus (P) deficiency. Means labelled with the same letter are not significantly different at the 5% significance level according to the Duncan's multiple range test. Error bars indicate the standard error of the means (n = 4)

Exudation of proton and total acid from roots under P deficiency. Wheat plants exuded H$^+$ and organic acid was found under P deficiency (Figure 3), but not under abundant P supply. The H$^+$ exudation rate was the highest for April Bearded, whilst A35–213 and Farah showed the lowest H$^+$ exudation rate (Figure 3a). Organic acid exudation was the highest for Hindy62, intermediate for Hankkijan Tapio, Dacke and April Bearded, and lowest for A35–213 and Farah (Figure 3b).

Plant growth, biomass allocation and starch content. Analysis across the P treatments showed that the shoot DM was similar among genotypes (Table 1), while April Bearded and Hindy62 had the significantly highest root DM compared with other genotypes. The root:shoot ratio was significantly higher for Farah, April Bearded, Hindy62 and Dacke than A35–213 and Hankkijan Tapio. When analysed across the genotypes, plants under the abundant P supply had significantly higher shoot and root DM than plants under the deficient P supply. However, the root-shoot ratio was significantly lower under the abundant than the deficient P supply. The starch content in the shoots was significantly higher in the deficient P than in the abundant P supply (Table 1), but was not significantly different among genotypes.

Macro- and micronutrient concentration and uptake. The concentrations and uptake of most of the nutrients were similar among genotypes (Tables 2 and 3). When analysed across the genotypes, the concentrations of macro- and micro-

Table 1. Summary of two-way analysis of variance on the shoot and root dry matter (DM), root: shoot ratio and starch content of six spring wheat genotypes under abundant and deficient phosphorus (P) supply

Factor		Shoot DM (mg)	Root DM (mg)	Root:shoot ratio	Starch concentration (%)
P level	abundant P	1.69 ± 0.10^a	0.40 ± 0.03^a	0.24 ± 0.01^b	1.32 ± 0.12^b
	deficient P	0.33 ± 0.01^b	0.17 ± 0.00^b	0.54 ± 0.02^a	2.26 ± 0.16^a
	P-value	< 0.001	< 0.001	< 0.001	< 0.001
Genotype	A35-213	1.04 ± 0.28	0.22 ± 0.03^c	0.30 ± 0.05^b	1.53 ± 0.31
	Farah	0.87 ± 0.23	0.28 ± 0.05^{ab}	0.43 ± 0.06^a	1.83 ± 0.32
	April Bearded	1.15 ± 0.31	0.34 ± 0.06^a	0.40 ± 0.06^a	1.60 ± 0.22
	Hindy62	1.08 ± 0.31	0.36 ± 0.08^a	0.47 ± 0.08^a	1.81 ± 0.25
	Hankkijan Tapio	0.93 ± 0.26	0.22 ± 0.04^c	0.31 ± 0.05^b	2.39 ± 0.40
	Dacke	0.99 ± 0.31	0.30 ± 0.06^{ab}	0.41 ± 0.06^a	1.58 ± 0.22
	P-value	0.633	0.032	< 0.001	0.150

Values are means ± the standard error of the means (n = 4). Means labelled with the different letters are significantly different at the 5% significance level according to the Duncan's multiple range test

Table 2. Summary of two-way analysis of variance on the concentrations of macro- and micronutrients in shoots of six spring wheat genotypes under abundant and deficient phosphorus (P) supply. Values are means ± the standard error of the means ($n = 4$). Means labelled with the different letters are significantly different at the 5% significance level according to the Duncan's multiple range test

Factor		Macronutrients (mg/kg)						Micronutrients (mg/kg)				
		N	P	K	Ca	Mg	S	Fe	Mn	Cu	Zn	B
P level	abundant P	27457 ± 1873^{a}	9029 ± 1110^{a}	55980 ± 2196^{a}	4086 ± 126^{a}	2936 ± 92^{a}	3610 ± 79^{a}	65.9 ± 2.5^{a}	134.9 ± 10.0^{b}	17.0 ± 0.5^{a}	157.5 ± 8.7^{b}	2.4 ± 0.1
	deficient P	27457 ± 497^{b}	1030 ± 118^{b}	35797 ± 721^{b}	2372 ± 89^{b}	2108 ± 56^{b}	1963 ± 33^{b}	55.5 ± 2.2^{b}	276.6 ± 7.8^{a}	13.0 ± 0.4^{b}	279.8 ± 10.0^{a}	2.3 ± 0.2
	P-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.004	< 0.001	< 0.001	< 0.001	0.468
Genotype	A35-213	34364 ± 2506	4663 ± 1743	43946 ± 4436	3020 ± 228^{bc}	2441 ± 125	2610 ± 211	59.7 ± 4.0	203.7 ± 28.6	14.3 ± 1.0	201.8 ± 23.8	3.3 ± 0.2^{a}
	Farah	35305 ± 3664	5356 ± 2363	50380 ± 5481	3746 ± 364^{a}	2521 ± 186	2794 ± 335	56.3 ± 3.6	187.4 ± 27.8	14.2 ± 0.9	214.3 ± 29.0	2.1 ± 0.1^{cd}
	April Bearded	35551 ± 3296	5077 ± 1914	46176 ± 4623	3250 ± 396^{b}	2340 ± 199	2884 ± 393	63.2 ± 3.9	200.5 ± 32.9	14.1 ± 1.3	207.6 ± 25.3	1.9 ± 0.2^{d}
	Hindy62	36626 ± 3395	5566 ± 2548	46708 ± 5062	3289 ± 320^{b}	2565 ± 238	2835 ± 310	63.5 ± 6.1	194.5 ± 34.1	16.8 ± 0.9	224.4 ± 35.6	2.5 ± 0.2^{b}
	Hankkijan Tapio	33304 ± 3154	4985 ± 2032	43510 ± 4433	2679 ± 300^{c}	2509 ± 183	2810 ± 316	67.3 ± 4.0	224.6 ± 29.2	14.8 ± 1.0	254.0 ± 29.4	2.4 ± 0.1^{cd}
	Dacke	34844 ± 3437	4533 ± 1722	44613 ± 4361	3391 ± 489^{ab}	2758 ± 258	2786 ± 374	54.1 ± 4.4	223.9 ± 31.9	15.7 ± 1.4	210.1 ± 22.4	2.0 ± 0.^{2d}
	P-value	0.815	0.997	0.633	< 0.001	0.342	0.429	0.228	0.481	0.130	0.265	< 0.001

nutrients in the shoots were significantly higher under the abundant P than under the deficient P supply except for Mn and Zn (Table 2). The uptake of macro- and micronutrients in the shoots was significantly higher under the abundant P than under the deficient P supply (Table 3).

DISCUSSION

The genotypic variations of root system structure and root hairs under contrasting P supply. Analysis across the P treatments showed that there were significant genotypic differences in root (root length, surface area and diameter) and root hair (length and density) traits (Figures 1 and 2). Root traits were significantly positively and linearly correlated with the uptake of macro- and micronutrients (data not shown), indicating the importance of root traits in nutrient acquisition (Nielsen 1979, Wang et al. 2016). Consequently, the greater root length and surface area could have contributed to the high uptake of many of the nutrients, especially N, P and K for April Bearded and Hindy62, though there was no statistical difference. Similar positive correlations were, however, not found between root hair traits and nutrient uptake, implying that root length and surface area play a more important role than root hairs in facilitating nutrient uptake (Wang et al. 2016). In addition to root system structure and root hairs, another root trait that may be related to P uptake is rhizosphere modification by root exudates, including protons and organic acids, which can mobilize P from bound soil P pools (Gahoonia and Nielsen 2004). In the current study, April Bearded exuded significantly more H^+ into solution than any other genotype, while Hindy62 exuded significantly more organic acids compared to the other genotypes (Figure 3). This could facilitate the uptake of nutrients particularly the immobile nutrient like phosphorus in the soil for April Bearded and Hindy62. Crop cultivars that can increase root exudation can enhance mineral nutrient uptake and assimilation, potentially boosting crop yields (Dakora and Phillips 2002). In common bean, Yan et al. (2004) found that root hair length and density were correlated with greater acid exudation. In the present study, H^+ exudation was significantly positively correlated with root length, while root hair length was more closely associated with total acid exuda-

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Table 3. Summary of two-way analysis of variance on the uptake of macro- and micronutrients in shoots of six spring wheat genotypes under the abundant and deficient P supply. Values are means ± the standard error of the means ($n = 4$). Means labelled with the different letters are significantly different at the 5% significance level according to the Duncan's multiple range test

	Factor	Macronutrients (mg/plant)						Micronutrients ((µg/plant)				
		N	P	K	Ca	Mg	S	Fe	Mn	Cu	Zn	B
P level	abundant P	70.3 ± 3.4^{a}	15.0 ± 2.0^{a}	92.2 ± 5.0^{a}	6.8 ± 0.4^{a}	4.8 ± 0.3^{a}	6.2 ± 0.4^{a}	109.9 ± 6.6^{a}	209.1 ± 6.1^{a}	28.1 ± 1.5^{a}	251.0 ± 9.9^{a}	4.0 ± 0.2^{a}
	deficient P	8.9 ± 0.2^{b}	0.3 ± 0.0^{b}	11.6 ± 0.3^{b}	0.8 ± 0.0^{b}	0.7 ± 0.0^{b}	0.6 ± 0.0^{b}	18.0 ± 0.9^{b}	89.9 ± 3.7^{b}	4.2 ± 0.1^{b}	90.2 ± 3.6^{b}	0.8 ± 0.1^{b}
	P-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Genotype	A35-213	39.3 ± 11.7	7.7 ± 3.8	52.2 ± 16.5	3.5 ± 1.0	2.6 ± 0.7	3.1 ± 1.0	63.5 ± 17.2	155.9 ± 23.1^{a}	16.0 ± 4.7	168.5 ± 32.1	3.0 ± 0.7
	Farah	34.6 ± 11.0	7.4 ± 4.0	49.2 ± 16.2	3.8 ± 1.2	2.4 ± 0.7	2.9 ± 0.9	49.8 ± 13.6	123.4 ± 23.5^{b}	12.6 ± 3.6	146.6 ± 28.5	1.9 ± 0.5
	April Bearded	46.1 ± 13.9	8.9 ± 3.9	60.8 ± 18.5	4.5 ± 1.4	3.0 ± 0.9	4.1 ± 1.4	79.0 ± 23.4	158.6 ± 23.1^{a}	18.4 ± 5.5	185.1 ± 36.6	2.3 ± 0.7
	Hindy62	44.6 ± 13.7	9.5 ± 5.0	58.0 ± 18.7	4.0 ± 1.3	2.9 ± 0.9	3.7 ± 1.2	71.5 ± 22.3	141.1 ± 24.4^{ab}	18.7 ± 5.4	172.0 ± 32.8	2.7 ± 0.7
	Hankkijan Tapio	34.4 ± 10.6	6.3 ± 2.7	44.0 ± 13.0	2.9 ± 1.0	2.6 ± 0.8	3.1 ± 1.1	61.8 ± 17.0	161.0 ± 22.9^{a}	14.2 ± 4.0	188.3 ± 32.0	2.3 ± 0.7
	Dacke	38.5 ± 12.6	6.4 ± 2.7	47.3 ± 14.8	4.1 ± 1.5	3.1 ± 1.0	3.5 ± 1.4	58.1 ± 19.0	156.8 ± 25.5^{a}	16.9 ± 5.5	163.2 ± 34.7	2.2 ± 0.8
	P-value	0.215	0.944	0.358	0.280	0.585	0.610	0.133	0.014	0.082	0.263	0.190

tion ($P = 0.20$) (data not shown), suggesting that root length is the most important determinant of H^+ exudation. Root hairs are more associated with mediating the release of organic acids and of acid, such as citrate (Narang et al. 2000) and acid phosphatase (Gahoonia et al. 2001).

Responses of root and root hair traits to P deficiency. The plants under the deficient P supply suffered from severe P stress, which resulted in reduced root and shoot growth (Table 1). However, the root:shoot ratio was significantly increased under P deficiency supply (Table 1), which is in good agreement with previous studies (Lynch 1995). Moreover, deficiency of P resulted in not only significantly lower tissue P concentration and uptake, but also lower concentrations of most other nutrients. A possible explanation for this is higher starch contents lowering nutrient concentrations under the P deficiency (Table 1).

Root hairs and root length responded differently to differences in P supply. When P concentration increased from 2 µmol or 200 µmol, RHD and TLRH decreased significantly except for RHD in Hankkijan Tapio, which is in good agreement with previous studies (Ma et al. 2001). Higher root hair densities under P deficiency arise from increased number of epidermal cells that differentiate into trichoblasts (Ma et al. 2001). The reduced density of root hairs under abundant P supply could decrease the root's ability to exploit the soil in its vicinity. In maize, Zhu et al. (2010) observed that low P availability significantly increased root hair length and P uptake in some inbred lines, but not in others. However, in the present study, analysis across the genotypes showed that RHL was not affected by the P supply, indicating that root hair density is a more P-regulated and P-responsive trait than root hair length in spring wheat. The extrusion of protons (Shen et al. 2004) and organic acids (Tang and Rengel 2003) from roots were enhanced under P deficiency, which did not occur under the abundant P condition.

In conclusion, higher genotypic variability was found for root hair than root system traits among the six analysed spring wheat genotypes. Root vigour traits were more closely associated with nutrient uptake. Deficiency of P depressed growth of root and shoot, and also decreased concentration of P and most other macro- and micronutrients. Root hair density appears more P-regulated and P-responsive than root hair length, and April

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Bearded exhibited the highest proton excretion and Hindy62 the highest organic acid excretion, which are traits that may be deployed for plant breeding to improve P efficiency of wheat.

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