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The effect of semi-dwarf genes on root system size in field-grown barley

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Abstract Root system size (RSS) was measured in 12 diverse barley genotypes and 157 double-haploid lines (DHs), using electric capacitance. The parents of the DHs, Derkado and B83-12/21/5, carry different semi-dwarfing genes, *sdw1* and *ari-e*.GP, respectively. Estimates of RSS were taken in the field thrice during plant development: stem elongation (RSS1), heading (RSS2) and grain filling (RSS3). The 12 barley genotypes were assessed over 3 years and at two or three locations each year; the DH mapping population was assessed at two locations in 2002. Among the 12 barley genotypes, those with the semi-dwarf genes had greater RSS values in all 3 years (28.9, 24.6 and 15.0% in years 1, 2 and 3, respectively) compared to non-semi-dwarf controls. The DH population showed transgressive segregation on both sides of the parent means, indicating polygenic control of RSS. Quantitative trait loci (QTLs) for RSS were found on five of the seven chromosomes: 1H, 3H, 4H, 5H and 7H and these were compared with previously mapped agronomic traits. The TotalRSS QTL on 3H was associated with *sdw1* and QTLs for height, plant yield and plant weight. The RSS3 QTL on 5H was associated with *ari-e*.GP and QTLs for height, plant yield, plant weight, harvest index and tiller number. The RSS3 QTL on 7H was also associated with a TotalRSS QTL and QTLs for plant weight and harvest index. Other RSS QTLs were not associated with any other trait studied. RSS is considered to be a polygenic trait linked to important traits, in particular to yield. The study highlights the effects of semi-dwarfing genes and discusses the potential for breeding for root traits.

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Introduction

There are a number of studies that relate root structure with environment. These are wide ranging and include the effects of biotic and abiotic stresses, spatial exploitation of roots in soil profiles, nutrient acquisition, rhizosphere interactions and hormone and other chemical effects on roots systems. Root system size (RSS) has been correlated with patterns of soil exploitation, efficiency and potential (Berntson 1994), and it has been suggested that cereal yields are associated with the abundance of finer roots occurring at deeper soil horizons than at surface soil layers (King et al. 2003). Agronomic characters of upland rice include a deep root system as well as tall stature, thick stems and few tillers (Ling et al. 2002).

Although there are several wide-ranging studies on the effects of environmental factors on root structure and function, to our knowledge studies on genetic controls in barley are limited. There have, however, been several quantitative trait loci (QTLs) studied for root traits in rice (Champoux et al. 1995; Ray et al. 1996; Price and Tomos 1997; Yadav et al. 1997; Kamoshita et al. 2002; Li et al. 2005). Forster et al. (2000) and Ellis et al. (2002) reported QTLs for δ^{15}N in the roots and root weight of 6-week-old barley seedlings. More recently, Forster et al. (2005) reported seminal root QTLs in 10-day-old barley seedlings for root number, root spread and root length. The studies of Forster et al. (2005) and Ellis et al. (2002) were based on controlled environment experiments, 2D observation chamber and hydroponics, respectively. Here we investigate older (nodal) root systems in field-grown material using electrical capacitance as a surrogate for RSS (Chloupek 1972, 1977). We have selected material to study the effects of semi-dwarf genes on RSS in barley. These genes have been used widely in the last decades in barley breeding throughout the world, particularly in Europe. The phenotype produced has shorter stems, lower weight of aerial mass and therefore higher harvest index compared to non-semi-dwarfs. Despite the importance of semi-dwarf cereals, little is known about their root systems and there has been no evaluation of their RSS. The *ari-e*.GP (syn. *Gpert*) dwarfing gene was produced by gamma ray irradiation of the cultivar Maythorpe in the UK in 1956. The highly successful malting quality cultivar Golden Promise was developed as a direct mutant (described in Sigurbjornsson and Micke 1969). The *ari-e*.GP dwarfing gene is, however, also associated with undesirable effects on economically important characters such as grain size and has now been superseded by the *sdw*1 dwarfing gene in most European semi-dwarf spring barleys. The *sdw*1 (syn. *denso*, Hellewell et al. 2000) dwarfing gene was also induced by mutation and a number of allelic variants have been produced (Haahr and von Wettstein 1976). The common *sdw*1 allele deployed in European barley was achieved by X-ray irradiation of the cultivar Valticky, which gave rise to the direct semi-dwarf mutant cultivar Diamant, developed in the Czech Republic in 1965. The purpose of the current work was to investigate the effects of these commercially important developmental genes on RSS, initially by a study of a range of barley genotypes followed by a study of a mapping population that segregated *ari-e*.GP and *sdw*1 dwarfing genes to investigate associations in detail.

Materials and methods

Plant material and environments

The RSS of a range of barley genotypes, with and without the semi-dwarf genes *ari-e*.GP and *sdw*1, was evaluated in field conditions at two or three locations using two sowing densities (5×10 and 10×10 cm) in 2001–2003 seasons. Evaluated genotypes for each year are given in Table 1.

The experiment was carried out at two locations in the Czech Republic, Zelesice and Branisovice, 60 km apart, on loamy soil. In 2003, a third location was added, Brno (also on loamy soil, 25 km from Zelesice). Sowing dates for Branisovice: 2 April 2001, 12 March 2002 and 17 April 2003; for Zelesice: 5 April 2001, 13 March 2002 and 17 April 2003; and for Brno 14 April 2003. Each combination of the three main factors (genotype, location and sowing density) was randomised in a trial grown in two replications, each plot of which consisted of five plants in 2001 and 2002. In 2003, the number of replications was increased to four, each of five plants. The RSS of individual plants in the plots was measured at three developmental stages: stem elongation (growth stage 31–34), heading (GS51-59) and grain filling (GS73-83). In 2002, RSS measurements at the third stage could not be taken at Branisovice due to lodging of the trial; and in Zelesice the RSS values were very small due to pre-mature ripening. The three growth stages occurred at similar times in each season: at weeks 5–7, 8–10 and 10–13 after sowing for stem elongation, heading and grain filling, respectively. The last sampling occurred 2–3 weeks before harvest.

A population of 156 Derkado × B83-12/21/5 doubled haploid lines (DHs), plus the two parents, was evaluated at two locations (Zelesice, Branisovice) in 2002, i.e. 1,896 plants were evaluated in a randomised complete block experiment (158 genotypes × 3 plants per genotypes × 2 replications × 2 locations) and assessed at the same three growth stages as mentioned earlier. The data were analysed to derive an overall mean for each DH line from the first two RSS measurements at Branisovice and Zelesice. As mentioned previously, further data could not be gathered from the Branisovice site in 2002; so the mean for the third measurement was derived from the Zelesice site only (RootMass3). At this latter site, mature plants were harvested and measured for overall plant height (cm), number of fertile stems (Tillers), overall weight of plants and seed (g) (PlantWt and PlantYld, respectively) from which harvest index (HIndex) was derived. No genotype × site interaction

Table 1 Evaluated varieties and experimental lines

Genotype	Dwarfing gene present	Comment
Derkado	*sdw*1	European cultivar, parent of a DH population
B83-12/21/5	*ari-e*.GP	European breeding line, parent of a DH population
Derkado × B83-12/21/5 DHs	Segregation for *sdw*1 and *ari-e*.GP	A doubled haploid mapping population
Tadmor	None	Selection from a Syrian landrace, parent of a RIL mapping population with ER/APM
ER/APM	None	Selection from Tunisia, parent of a RIL mapping population with Tadmor
Chime	*sdw*1	UK cultivar
Mehola	None	Wild barley, *H. spontaneum* from Israel
Valticky	None	Old Czech cultivar, parent of Diamant
Diamant	*sdw*1	Induced semi-dwarf mutant of Valticky
Canada Park (HS92)	None	Wild barley, *H. spontaneum* from Israel
Jersey	Probably *sdw*1	Modern EU cultivar of medium height with excellent malting characters
Malz	Probably *sdw*1	Recently released EU semi-dwarf malting cultivar

was detected for the first two measurements of RSS, so the data were combined over sites and measurements (TotalRSS).

Evaluation of RSS and statistical evaluation

RSS was evaluated by electrical capacitance measured in relation to the surrounding soil (Chloupek 1977). The electrical capacitance is presumed to be formed by polarisation of living membranes and/or living cells, where the plant provides the first plate and the soil the second plate of a capacitor. During the measurements one clamp of the C-meter was connected to all basal parts of the stalks of an individual plant, the second electrode was grounded in the middle of the spacing (between individual plants). Dry leaves that did not conduct current were carefully removed from the basal parts. The results are of relative nature. Such values are comparable only when plants of the same plant species are grown in the same substrate, at the same soil moisture (on the same day without precipitation) and compared at the same time. When the measured aerial parts are dry, the measurement is not influenced by contact with neighbouring plants.

The results were evaluated by analysis of variance and by regression analysis. The percentages of particular experimental factors are expressed as standard deviations for genotype (i.e. "heritability"), sowing density and location, and experimental error (unexplained variation), respectively, of the total standard deviation (=100%) found in the experiment.

Mapping studies

Twenty-four additional markers have been scored on the Derkado × B83-12/21/5 population since publication of the previous map (Ellis et al. 2002). Two of these were additional genomic SSRs and the remaining 22 were EST-derived markers, either as SSRs (Ctig) or as single nucleotide polymorphisms (SNP or abc). Joinmap 3.0 (Van Ooijen and Voorrips 2001) was used to produce a revised genetic map of the Derkado × B83-12/21/5 population, which included the additional markers, ignoring any previous map order information. The phenotypic means of the height, yield and RSS characters were then combined with the mapping data to scan for QTLs using PLABQTL (Utz and Melchinger 1996). The program defaults were used to identify significant co-factors for the phenotypic characters, and those that were associated with any QTLs that failed to exceed a LOD threshold of 2.5 were iteratively removed. Permutation was then used to establish the LOD for a 5% error threshold for the whole experiment and further iterative co-factor removal carried out if necessary. The presence of any significant epistatic effects was tested and then cross-validation was used to estimate the overall amount of phenotypic variation accounted for by the QTLs detected.

Results

Individual means of each genotype, the percentage of variation attributed to them ("heritability"), the effects of sowing density and location and the experimental error are given in Table 2. Genotypic differences were greatest in the later two measurements in 2001 and the last measurement in 2002 and therefore accounted for the greatest amount of variation. For the remaining measurements, genotypic differences were relatively small and, with the exception of the first measurement in 2002, location differences accounted for the greatest portion of the variance. Overall, experimental error variation never exceeded 5% of the total. RSS was influenced, at all three stages, by genotype × locations and genotype × sowing density interactions (Table 2).

Genotypes in 2001

The smallest RSS values were found for ER/APM and Mehola. The largest RSS values were provided by Chime, B83-12/21/5 and Derkado (all three are semi-dwarfs) at stem elongation and by B83-12/21/5 (also semi-dwarf) at heading and grain filling. The modern germplasm had greater RSS values than the landrace and the wild barley genotypes tested. Although, RSS at both sowing densities differed significantly only at the third growth stage (grain filling) when demand for resources was probably the largest. However, RSS was greater at the lower sowing density (larger plant spacing) for all growth stages, the differences were only significant at RSS3.

Genotypes in 2002

Average RSS (Table 2) of the four genotypes with the semi-dwarf genes was greater by 11.2 and 38.0% than the RSS of other four genotypes tested at the first and second growth stages, respectively. The RSS values for Diamant were greater than Valticky, its 'isogenic' parental line. Although Diamant was produced by induced mutation of Valticky (Bouma 1967) and therefore theoretically isogenic, recent studies have shown that comparisons of current accessions are not so close (Mlcochova et al. 2004); there are several accessions of Diamant that have arisen over 40 years of multiplication. The percentage of the variance for genotype of the total variance ("heritability") amounted to 14.8 and 23.2% for stages 1 and 2, respectively, and the percentage of the standard error amounted to 4.3 and 5.0%, respectively.

Genotypes in 2003

Average RSS of Diamant, with the *sdw*1 semi-dwarf gene, was greater than Valticky at all growth stages (6.4,

Table 2 Comparison of RSS (pF.10^5) of the evaluated varieties in 3 years (2001–2003) each in three terms (1: shoot elongation; 2: heading; 3: grain filling)

Variety (semi-dwarf gene)	2001			2002		2003		
	1	2	3	1	2	1	2	3
Derkado (*sdw*1)	33.8^{bc}	46.8^{c}	32.5^{c}	13.1^{d}	30.6^{e}	–	–	–
Chime *(sdw1)*	35.1^{c}	43.0^{b}	30.1^{c}	12.9^{cd}	29.7^{de}	–	–	–
B83 (*ari-e*.GP)	34.0^{bc}	51.0^{d}	36.1^{d}	9.3^{a}	24.3^{cd}	–	–	–
Tadmor	31.8^{b}	40.8^{b}	25.5^{b}	10.6^{b}	16.0^{a}	–	–	–
ER/APM	27.2^{a}	34.7^{a}	22.2^{a}	9.4^{ab}	20.6^{b}	–	–	–
Mehola	32.1^{b}	33.8^{a}	20.3^{a}	–	–	–	–	–
HS 92	–	–	–	11.8^{c}	20.6^{b}	–	–	–
Diamant (*sdw*1)	–	–	–	12.4^{cd}	27.3^{d}	50.0^{a}	49.3^{c}	21.1^{b}
Valtický	–	–	–	11.1^{bc}	23.9^{c}	47.0^{a}	44.2^{ab}	16.6^{a}
Jersey	–	–	–	–	–	44.8^{a}	42.3^{ab}	17.8^{a}
Malz	–	–	–	–	–	46.3^{a}	41.8^{a}	16.2^{a}
LSD $P < 0.05$	0.98	1.02	0.97	1.17	2.99	3.96	3.04	1.68
Heritability (%)	18.3	35.1	38.3	14.8	23.2	7.4	12.4	9.7
Effect of density (%)	6.5	7.7	19.9	32.0	21.4	1.9	24.0	12.4
Effect of locations (%)	38.2	16.1	2.2	15.0	9.4	60.1	34.6	47.3
Accuracy (%)	3.7	4.5	4.8	4.3	5.0	4.8	3.9	2.6

Mean values marked in the same column by the same superscripted letter did not differ significantly ($P < 0.05$). The values in the last four rows are expressed as percentages of the roots of the mean squares for the factors of the root of the total mean square. Accuracy = standard deviation of the experimental error

Forty plants were averaged for the mean values of the varieties in 2001 and 2002 and 120 in 2003

11.5 and 27.1% at stem elongation, heading and grain filling, respectively, Table 2). The two modern malting quality cultivars Jersey and Malz had smaller RSS than Diamant, suggesting that the effect of *sdw*1 may be tempered by genetic background. The percentage of the variance for genotype of the total variance amounted to 7.4, 12.4 and 9.7% in the first, second and third growth stages, and the percentage of standard error was 4.8, 3.9 and 2.6%, respectively.

Evaluation of DH mapping population and genetic correlations

There was highly significant genetic variation for TotalRSS in the DH population. The RSS of Derkado (*sdw*1) was greater than that of B83-12/21/5 (*ari-e*.GP). Most of the DH lines showed transgressive segregation above that of either parent, suggesting possible epistatic effects. Considering the two measurement stages separately, the mid parent was significantly less than the DH mean for the first measurement but not for the second, suggesting that any epistatic effects occurred in early root systems.

Average RSS was evaluated in relation to the others traits. Since the DHs are completely homozygous and genetically distinct, any correlation infers a genetic association. Highly significant ($P < 0.01$) correlations were found for RSS with: plant height, aerial weight, average number of spikes (i.e. with number of fertile tillers) and grain yield ($r_G = 0.192$, 0.420, 0.355 and 0.209, respectively). Tightness of the relation between average RSS and the four characters given above increased during plant development; its average value was: $r_G = 0.123$ at stem elongation, $r = 0.204$ at heading and $r = 0.510$ at grain filling.

QTL mapping

Nineteen QTL were detected for the seven characters studied, ranging from four for Height and TotalRSS to one for Tillers, accounting for between 84 (Height) and 13% (RSS3) of the phenotypic variation in the characters after cross validation (Table 3). Derkado QTL alleles in the region of *sdw*1 decreased height, plant weight and yield but increased TotalRSS (Fig. 1). This QTL was detected for both the overall mean of RSS1 and RSS2 (data not shown) but was most significant for the earlier score, suggesting that the dwarfing gene carried by Derkado is either linked to an allele at another locus that increases early root development or that this is a pleiotropic effect of the dwarfing gene. In contrast Derkado QTL alleles in the region of *ari-e*.GP increased height, tiller number, plant weight and yield and RSS3 but reduced harvest index. A third region affecting a number of characters was located on chromosome 7H in the interval P25M42c to P16M47f, where Derkado QTL alleles decreased plant weight, TotalRSS and RSS3 but increased harvest index. Two other QTL were detected for TotalRSS with the Derkado allele decreasing expression of the character at both, notably in the region of *mlo* on chromosome 4H, suggesting an association of the *mlo*11 powdery mildew resistance allele carried by Derkado with decreased early root formation (Fig. 1). No epistasis was detected between the QTLs for any of the characters measured in the experiments, whether or not TotalRSS was broken down into its two stage components.

Table 3 Summary of the QTLs detected for height, yield components and RSS in Derkado × B83-12/21/5 population

Character	Chromosome	Left marker	LOD	Additive effect	5% Threshold[a]	Phenotypic variation[b]
Height	3Hb	abc08541	33.93	−6.9	2.9	84.2
Height	4H	HVM3	4.29	−2.6		
Height	5H	ari-eGP	52.56	10.3		
Height	7H	Bmag341	8.35	2.9		
Hindex	5H	Bmag337	3.77	−0.021	3.0	28.6
Hindex	7H	P25M42c	10.23	0.033		
Tillers	5H	ari-eGP	6.51	0.97	2.8	12.5
PlantWt	3Hb	abc08541	9.61	−4.16	2.9	55.3
PlantWt	5H	ari-eGP	27.28	8.20		
PlantWt	7H	P25M42c	3.56	−2.62		
PlantYield	3Hb	abc08541	11.77	−1.15	2.9	48.8
PlantYield	5H	ari-eGP	22.51	1.70		
PlantYield	6H	P31M40a	3	0.61		
Total RSS (All)	1Ha	E52M48c	4.53	−2.57	3.0	28.1
Total RSS (All)	3Hb	BMag0606	5.3	2.42		
Total RSS (All)	4H	mlo	5.11	−2.37		
Total RSS (All)	7H	P25M42c	3.44	−1.98		
RootMass3	5H	Ari-eGP	5.79	1.00	2.9	12.8
RootMass3	7H	P25M42c	3.16	−0.76		

[a] LOD threshold for a 5% genome wide error rate after 1,000 permutations

[b] Percentage phenotypic variation accounted for by detected QTLs after cross-validation

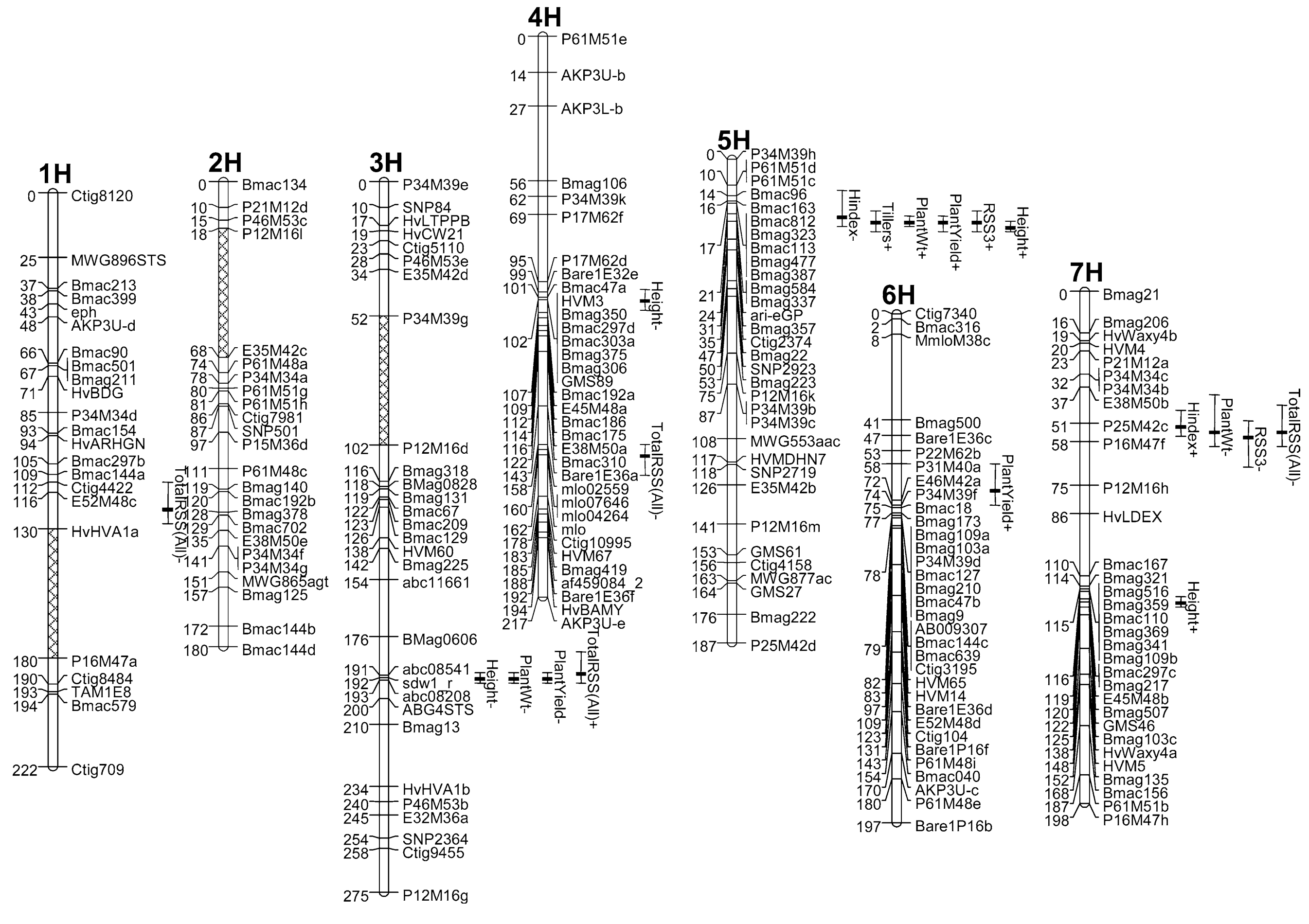

Fig. 1 QTL map of Derkado × B83-12/21/5 population. *Thick line* indicates QTL peak and *whiskers* indicate 1 LOD confidence interval

Discussion

Dalton (1995) stated that the electrical capacitance method for RSS evaluation showed considerable promise. Beem et al. (1998) found that capacitance meters equipped with a clamp for rapid attachment to the plant might facilitate the non-destructive identification of genotypes with root characteristics that confer adaptation to various environments. Conditions for accurate capacitance measurements included a moist medium around the plant root system and a consistent placement of the electrode. Roots systems of several species have been assessed using electrical capacitance: maize, sunflower, oat, onion, rapeseed, alfalfa, white clover, potato, apple (Chloupek 1972, 1977; Chloupek and Rod 1985; Chloupek et al. 2003; Psarras and Merwin 2000) and now barley. The method is simple and the data obtained here proved to be robust and suitable for genetic mapping studies.

The comparison of genotypes (Table 1) indicated a general trend of increasing RSS values from wild barley to landrace barley to modern cultivars, suggesting that root traits have been involved in domestication and selection of the barley crop, albeit inadvertently. Wild barley has also been reported to have few seminal roots with a narrower spread than cultivated genotypes (Gordon et al. 2005). Large genetic variation therefore exists for root traits in the barley gene pool. The difference in RSS between Diamant and Valticky is interesting as this may be attributed to the *sdw*1 mutation induced by X-ray irradiation (Bouma 1967), with Diamant producing consistently greater RSS values at all growth stages over the 2 years tested than Valticky. However, the comparisons of Diamant with Valticky need to be treated with some caution as the lines tested are not completely isogenic, due to divergence during 40 years of multiplication of the two lines (Mlcochova et al. 2004).

The QTL analysis included some characters that had previously been mapped on the Derkado × B83-12/21/5 population, namely height and yield. The latter had been mapped from results obtained from the overall yields of DHs grown in plots whereas that of the current study was derived from single plant yields. The three loci for single plant yield were all in the same region as the previously described ones for plot yield (Thomas et al. 1998; Ellis et al. 2002), but the effect of the QTL in the region of *sdw*1 on chromosome 3H is opposite to that detected in plots. The dwarfing gene carried by Derkado was associated with increased plot yield (Thomas et al. 1998; Ellis et al. 2002) but with decreased single plant yield from the results of the current study. This could be due to environmental differences where the later heading of the *sdw*1 semi-dwarf types means that they are more susceptible to late season drought stress and their yield is likely to be reduced. Such an effect was indeed observed in rainfed trials of the Derkado × B83-12/21/5 population carried out in Egypt and Morocco (Forster et al. 2005). The height QTLs detected are all in line with previous observations (Thomas et al. 1998, unpublished data) and we can conclude that the agronomic observations from this experiment agree with previous studies and therefore can conclude that we are measuring real differences in root systems.

As might be expected, there is considerable environmental control on the RSS measures but the degree of genetic control is, nevertheless, surprisingly high (Table 3) suggesting that there are real opportunities to manipulate the expression of these characters through selection. The QTL analyses clearly highlight the importance of the two dwarfing genes in the genetic control of RSS, but it is interesting that they appear to operate at different stages and have different effects. The *sdw*1 gene increases RSS in the earlier growth stages, especially the first, whereas the *ari-e*.GP gene is only effective in the later stages and decreases RSS3. Whilst not consistent with the observed height effects, this is entirely consistent with the effects of each on development. The *sdw*1 gene delays stem elongation and heading whereas the *ari-e*.GP gene leads to earlier heading (Powell et al. 1985a, b; Thomas et al. 1995). Whilst these results are consistent with those of the parental survey from 2002, they are not consistent with those from 2001, where B83-12/21/5 had a significantly greater RSS3 than Derkado (Table 2). B83-12/21/5 is, however, very late heading for an *ari-e*.GP genotype and the observed effects could still be the result of developmental differences in different seasons. Although *ari-e*.GP was associated with reduced RSS in the QTL study, B83-12/21/5, which carries *ari-e*.GP exhibited some high RSS values compared with other barley lines (Table 2). This could be due to modifying effects of the genetic background such as the positive effects of the B83-12/21/5 allele on RSS on chromosome 7H (Fig. 1). Studies of matched pairs of lines or near-isogenics such as recombinant chromosome substitution lines (Young et al. 2004) could be used to study these issues more closely.

The results have parallels with those from rice root QTL studies. The region between RZ730 and RZ801 markers on chromosome 1 of rice is associated with QTLs for total root weight, deep root weight, deep root per shoot ratio and maximum root length (Yadav et al. 1997). This interval corresponds to the position of the *sd-1* semi-dwarfing gene (Huang et al. 1996). Other QTLs for height in rice (on chromosomes 2, 3, 8 and 9) were also associated with root traits. In this study both barley dwarfing genes were associated with a number, but different set of root QTLs. In addition, it is likely that the QTLs for Total RSS and RSS3 on 7H are also associated with a height gene, possibly an *erectoides* gene. The results therefore indicate strong interaction between shoot and root physiology (Klepper 1991). However, not all barley root QTLs were associated with height genes and this has also been found in rice (Yadav et al. 1997), sorghum (Yoshida and Hasegawa 1982) and wheat (Clarke and McCaig 1993).

The barley root system, and that of most small grain cereals, can be divided into two classes, seminal (arising from the seed) and nodal (arising from stem bases) (Hector 1936; Briggs 1978). Previous studies on seedlings, using the same population as here, mapped seminal root traits for root number, spread, length, (Forster et al. 2005), and weight and δ^{15}N (Ellis et al. 2002). All of these, apart from three root spread QTLs, were associated with one or other of the semi-dwarfing genes. The effect of the *ari-e*.GP gene was to reduce seminal root number, root length and root spread in 10-day-old seedlings (Forster et al. 2005) and to reduce root weight in 6 week old seedlings (Ellis et al. 2002). In the current QTL study *ari-e*.GP was also associated with reduced RSS3, this gene therefore appears to have pleiotropic effects on both the seminal and nodal root systems. It is interesting that *ari-e*.GP was also associated with reduced tiller number. Since the nodal system emanates from stem bases fewer tillers may have a direct effect on reduced RSS3. The *sdw*1 gene was not associated with any seminal root trait in previous studies, apart from weight and δ^{15}N (Ellis et al. 2002), but was associated with increased RSS in this study. The contrasts between seminal root QTLs and RSS (assumed to be composed mainly of nodal roots) suggest that different gene sets operate for each root system.

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References

Beem J. van, Smith ME, Zobel RW (1998) Estimating root mass in maize using a portable capacitance meter. Agron J 90:566–570

Bengough AG, Gordon DC, Al-Menaie HS, Allan D, Keith R, Thomas WTB, Forster BP (2004) Gel observation chamber for rapid screening of root traits in cereal seedlings. Plant Soil 262:63–70

Berntson GM (1994) Modeling root architecture—are there tradeoffs between efficiency and potential of resource acquisition? New Phytol 127:483–493

Bouma J (1967) New variety of spring barley, 'Diamant' in Czechoslovakia. In: Induzierte Mutationen und ihre Nutzung, Erwin Baur Gedachtnisvorlesungen IV, 1966, Abh Dt Akad Wiss Berl Akademie-Verlag, Berlin 2:177–182

Briggs DE (1978) Barley. Chapman and Hall Ltd, London, pp. 76–88; 419–441

Champoux MC, Wang G, Sarkarung S, Mackill DJ, O'Toole JC, Huang N, McCouch SR (1995) Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. Theor Appl Genet 90:969–981

Chloupek O (1972) The relationship between electric capacitance and some other parameters of plant roots. Biol Plant 14:227–230

Chloupek O (1977) Evaluation of the size of a plant's root system using its electrical capacitance. Plant Soil 48:525–532

Chloupek O, Rod J (1985) Combining ability of forage and seed productivity of alfalfa. Czech. Genetika a Slechtení 21:121–127

Chloupek O, Ehrenbergerová J, Opitz von Boberfeld W, Ríha P (2003) Selection of white clover (*Trifolium repens* L.) using root traits related to dinitrogen fixation. Field Crops Res 80:57–62

Clark JM, McCaig TN (1993) Breeding for efficient root system. In: Hayward MD, Bosemark NO, Ramagosa (eds) Plant breeding: principles and prospects. Chapman and Hall, London, pp 485–499

Dalton FN (1995) In-situ root extent measurement by electrical capacitance methods. Plant Soil 173:157–165

Ellis RP, Forster BP, Gordon DC, Handley LL, Keith R, Lawrence P, Meyer RC, Powell W, Robinson D, Scrimgeour CM, Young GR, Thomas WTB (2002) Phenotype/genotype associations of yield and salt tolerance in a barley mapping population segregating for two dwarfing genes. J Ex Bot 53:1–14

Forster BP, Ellis RP, Robinson D, Handley LL, Scrimgeour C, Thomas WTB (2000) QTL mapping of root traits in a doubled haploid population segregating for two dwarfing genes tested in control and salt stressed conditions. Barley Genet VIII 3:247–248

Forster BP, Thomas WTB, Chloupek O (2005) Genetic controls of barley root systems and their associations with plant performance. Aspects Appl Biol 73:199–204

Gordon DC, Bengough AG, Clark S, Al-Menaie H, Thomas WTB, Forster BP (2005) A phenotypic screen for genetic analysis of barley seedling root traits. Aspects Appl Biol 73:81–84

Haahr V, von Wettstein D (1976) Studies of an induced, high-yielding dwarf-mutant of spring barley. Barley genetics III, Proceedings 3rd international barley genetics symposium, Garching, 1975, pp 215–218

Haung N, Courtois B, Khush GS, Lin H, Wang G, Wu P, Zheng K (1996) Association of quantitative trait loci for plant height with major dwarfism genes in rice. Heredity 77:130–137

Hector JM (1936) Introduction to the botany of field crops; I. Cereals Central News Agency, Johannesburg, pp 234–271

Hellewell KB, Rasmusson DC, Gallo-Meagher M (2000) Enhancing yield of semidwarf barley. Crop Sci 40:352–358

Izumi Y, Kono Y, Yamauchi A, Iijima M (1997) Quantitative analysis of the architecture of seminal root system of rice (*Oryza sativa* L.) grown under different soil moisture conditions. Jap J Crop Sci 66:427–435

Kamoshita A, Wade LJ, Ali ML, Pathan MS, Zhang J, Sarkarung S, Nguyen HT (2002) Mapping QTLs for root morphology of a rice population adapted to rainfed lowland conditions. Theor Appl Genet 104:880–893

King J, Gay A, Sylvester-Bradley R, Bingham I, Foulkes J, Gregory P, Robinson D (2003) Modelling cereal root system for water and nitrogen capture: towards an economic optimum. Annals Bot 91:383–390

Klepper B (1991) Root-shoot relationships. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots, the hidden half. Marcel Dekker, New York, pp 265–286

Li Z, Mu P, Li C, Zhang H, Li Z, Gao Y, Wang X (2005) QTL mapping of root traits in a doubled haploid population from a cross between upland and lowland *japonica* rice in three environments. Thoer Appl Genet 110:1244–1252

Ling ZM, Li ZC, Yu R, Mu P (2002) Agronomic root characters of upland rice and paddy rice (*Oryza sativa* L.). J Chin Agric Univ 7:7–11

Mlochova L, Chloupek O, Uptmoor R, Ordon F, Friedt W (2004) Molecular analysis of the barley cv *Valticky* and its X-ray-derived semidwarf-mutant *Diamant*. Plant Breed 123:421–427

Powell W, Caligari PDS, Thomas WTB, Jinks JL (1985a) The effects of major genes on quantitatively varying characters in barley. 2. The denso and daylength response loci. Heredity 54:349–352

Powell W, Thomas WTB, Caligari PDS, Jinks JL (1985b) The effects of major genes on quantitatively varying characters. 1. The GP-ert locus. Heredity 54:343–348

Price AH, Tomos AD (1997) Genetic dissection of root growth in rice (*Oryza sativa* L.). II: mapping quantitative traits loci using molecular markers. Theor Appl Genet 95:143–152

Psarras G, Merwin IA (2000) Water stress affects rhizosphere rates and root morphology of young *Mutsu* apple trees on M.9 and MM.111 rootstocks. J Amer Soc Hort Sci 125:588–595

Ray JD, Yu L, McCouch SR, Wang G, Nguyen HT (1996) Mapping quantitative trait loci associated with root penetration ability in rice (*Oryza sativa* L.). Theor Appl Genet 100:697–712

Sigurbjornsson B, Micke A (1969) Progress in mutation breeding. In: Induced mutation in plants. Proceedings of an international symposium on nature, induction and utilization of mutation in plants. International Atomic Energy Agency, Vienna, 1969, pp 673–697

Thomas WTB, Baird E, Fuller JD, Lawrence P, Young GR, Russell J, Ramsay L, Waugh R, Powell W (1998) Identification of a QTL decreasing yield in barley linked to *Mlo* powdery mildew resistance. Molec Breed 4:381–393

Thomas WTB Powell W, Waugh R, Chalmers KJ, Barua UM, Jack P, Lea V, Forster BP, Swanston JS, Ellis RP, Hanson PR, Lance RCM (1995) Detection of quantitative trait loci for agronomic, yield, grain and disease characters in spring barley (*Hordeum vulgare* L.). Theor Appl Genet 91:1037–1047

Utz HF, Melchinger A (1996) PLABQTL: a program for composite interval mapping of QTL. J Agric Genom 2: http://www.ncgr.org/ag/jag/papers96/paper196/indexp196.html

Van Ooijen JW, Voorrips RE (2001) JoinMap®3.0, Software for the calculation of genetic linkage maps. Plant Research International, Wageningen, the Netherlands

Yadav R, Coutrois B, Huang N, McLaren G (1997) Mapping genes controlling root morphology and root distribution in a doubled haploid population of rice. Theor Appl Genet 94:619–632

Yoshida S, Hasegawa S (1982) The rice root system: its development and function. In: Drought resistance in crops with emphasis on rice. IRRI, Los Baños, The Philippines, pp 97–114

Young GR, Lawrence PE, Waugh R, Thomas WTB (2004) Construction of a barley chromosome substitution library. Book of abstracts, 9th international barley genetics symposium, Brno, Czech Republic