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RESEARCH ARTICLE

Uncommon selection by root system size increases barley yield

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Abstract Most agronomy practices such as fertilization, irrigation, and soil treatment involve plant root interactions. However, the role of plant roots is rarely assessed during agricultural experiments due to the lack of suitable methods. Plant varieties with a larger root system use soil water and nutrients in dry environments more effectively than varieties with a smaller root system. Such large root varieties can be developed by breeding. Therefore, we evaluated the effects of selection for large or small root systems in 12 barley populations developed via the mutual crossing of four parents in the F_3 generation as a response to selection in the preceding F_2 generation. Root system size was analyzed by measuring electrical capacitance. Results show that our selection method was effective because the progeny of plants with larger root systems also had larger root systems. Conversely, the progeny of plants with smaller root systems also had smaller root systems. The average differences were + 40 and −43 % in the parental segregating generation and +4 and −2 % in the progeny. The root system size impacted the grain yield, which showed a twofold greater response to selection. Indeed, plants with a root system increase of 3.9 % exhibited a yield increase of 8.1 %. Some varieties transmitted larger root systems to their progeny, and some transmitted smaller root systems. Thus, we show that the method used enabled the comparison of root system size in the same crop, in the same soil, and at the same time, which is particularly suitable for selecting root system size in practical breeding. We do not know any other suitable method for the repeated evaluation of intact plants and harvesting of seeds from the selected plants. Root system size has not yet been reported by other authors as a selection criterion in practical breeding, with the exception of root crops such as sugar beet and carrots.

Keywords Root system size · Barley · Inheritance · Varieties · Drought · Electrical capacitance · *Hordeum vulgare* L

1 Introduction

Climate change is a major issue for agricultural sustainability (Fleming and Vanclay 2010). The field of agronomy will be forced to change its adaptive capacity and develop flexible procedures that reflect rapidly changing agroclimatic conditions (Trnka et al. 2011). The positive effects of water and nutrient application on yields have led to the overuse of these practices in the last several decades. This misuse of irrigation and fertilizers is no longer sustainable, given the associated economic and environmental costs. The transpiration stream largely determines the availability of mineral N in the rhizosphere, which makes our poor ability to estimate root system density a major obstacle to the precise assessment of nitrogen availability to fertilized crops (Gonzales-Dugo et al. 2010). A larger investment by a crop in fine roots that are deeper in the soil and fewer roots in surface layers would improve yields by allowing plants to access extra resources (King et al. 2003). Bertholdsson and Kolodinska Brantestam (2009) showed the importance of early vigor for drought tolerance and development of finer roots in modern barley cultivars. Seminal root length and weight were related to grain yield in official variety trials in Sweden and Denmark. The economic return on the investment in roots for water capture is twice that for nitrogen capture, as documented by Palta et al. (2011), who showed that a larger root system down to a depth of 0.7 m resulted in significantly higher absorption of water and nitrogen. Relatively small amounts of subsoil water can be highly

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valuable for increasing grain yields (Kirkegaard et al. 2007) and support the use of selection for a greater root system size.

In this study, we evaluated the response to selection for intact root system size measured using electrical capacitance (Fig. 1). The response is the fraction of the selection difference in the parental population that is inherited into their progeny. High values indicate that the trait is mainly controlled by major genes, while low values indicate that it is controlled by quantitative trait loci and is therefore predominantly influenced by the environment (years and locations). The general combining ability is the ability of a parent to lead to larger root systems in progeny than that of the parents in most combinations when crossed with different parents.

2 Materials and methods

2.1 Plant materials and experimental site

The spring barley malting varieties Diplom, Jersey, Prestige, and Saloon were mutually crossed in 2010 in a diallel manner, i.e., each variety was crossed with all others, including reciprocally (as both mothers and fathers). The resulting 12 combinations reproduced in the winter of 2010/2011 in a greenhouse and were sown on April 21, 2011, in a field at the Hrubčice Plant Breeding Station (49°26′41.160″N, 17°11′54.940″E) in a fertile lowland (elevation, 210 m; 50-year average annual temperature, 8.5 °C; 50-year average annual rainfall, 578 mm; soil type, Haplic Chernozem with 38–39 % clay). Each combination of this F_2 generation was sown in three replicates between the two parents, each replicate consisting of a row of 12 plants spaced at 0.1×0.1 m (see Chloupek et al. 2006). The eight inner plants in each row were evaluated for root system size during the periods of stem elongation, heading, and grain filling on June 13 and July 5 and 18, respectively. Root evaluation was performed via electric capacitance, as described by Chloupek (1972). From each replicate in the 12 populations, we selected the two plants with the largest roots (selection A) and the two with the smallest (selection B). The plants were harvested on August 17, 2011. Seeds from six plants from selection A and six from selection B from each of the 12 combinations were bulked and sown in the following generation to evaluate the response to the applied selection. The F_3 generation was sown on March 27, 2012, in a similar manner, and again evaluated for root system size in the same developmental stages, stem elongation, heading, and grain filling on June 6 and 22 and July 9, respectively. The seeds were harvested on August 6, 2012.

Fig. 1 Measurement of cereal root system size on the basis of its electrical capacitance

2.2 Evaluation of root system size via electrical capacitance

We have previously developed and applied an electrical capacitance method for evaluating the size of the intact root system in soil. Chloupek (1972, reprinted in Chloupek et al. 2010) found significant correlations between electrical capacitance and the fresh and dry weight, volume, and surface area of roots in maize, sunflowers, oats, and onions. The results of this type of evaluation are relative in nature and comparable only when plants of the same species are grown in the same substrate with the same soil moisture (on a day without rain) and compared simultaneously. The surface of the aerial parts of the plants must be dry at the time of measurement so that the measurements are not influenced by any contact with neighboring plants.

One wire of the capacitance meter was connected by a clamp to all basal parts on the plant at the same height. This height was near the soil but not in contact with it. The second wire, which leads the measuring current to the soil, was grounded in the middle of square of plants in the same distance to the measured plants. An impedance bridge (LCR meter) was used and set for Cp (parallel measured capacitance) at a frequency of 1 kHz. Results are given in units of electrical capacitance, in nanofarads (nF).

The Dalton model (1995) has been the main concept (Ellis et al. 2012, 2013) used to understand equivalent root circuitry. This model proposes that roots are cylindrical capacitors, with the epidermis and xylem as the external and internal electrodes, respectively. It is thought that the entire root system contributes to the measured capacitance and that it is plausible to calculate the average permittivity of cortex tissue if the roots are assumed to be cylindrical capacitors (i.e., the Dalton model). The capacitance therefore varies in proportion to the root surface area, mass, length, and relative permittivity of the plant tissue.

A significant relationship between root system size and its electrical capacitance has been observed in several plant species (maize, sunflower, oats, onions, spinach, tomatoes, apples, poplars, and willows), as reported in five papers published by Chloupek et al. (2010). In addition, Dietrich et al. (2012) found a significant correlation between barley root system size and its capacitance in hydroponics, but when roots were raised out of solution, capacitances were not linearly related to submerged root mass. Excision of roots in the solution had a negligible effect on the measured capacitance. However, Ozier-Lafontaine and Bajazet (2005) reported a good linear correlation between root capacitance and the fresh weight of spinach roots (r^2=0.937) in a "root cutting" experiment, similar to results in a "progressively immersed root system" involving tomato plants (r^2=0.987). Our trials were not evaluated in hydroponics, but in soil in the field. The results were statistically evaluated by STATISTICA 7.0.

3 Results and discussion

3.1 Problems of measuring root system size

The isolation of intact living root systems from soil in fields has not been reported to date and may be impossible. The difficulty of this task is demonstrated by many observations. For instance, biomass estimates from minirhizotrons indicate that roots with a diameter of less than 0.25 mm account for nearly 95 % of the total root length of shrubby oaks (Brown et al. 2009). Additionally, root separation using a sieve with a 0.5-mm mesh screen leads to a marked underestimation of the root length density and root biomass. Values up to three times higher have been observed when using a 0.2-mm mesh screen compared with a 0.5-mm screen (Muňoz-Romero et al. 2010). We are unaware of any method that is suitable for the repeated evaluation of the same plant in different developmental stages and the evaluation of many plants in segregated populations, which is an important prerequisite for successful and practical breeding. Therefore, we used electrical capacitance for evaluations. Root system sizes were reported in our previous study as an average of three following measurements and in the present study as a sum of three following measurements to avoid problems with the rounding of values.

3.2 Root system size and crops

The average root system sizes of the parental varieties, of their 12 progeny in parental generation F_2, and of selected progeny in generation F_3 are shown in Tables 1 and 2.

Table 1 Average root system sizes (sum of three measurements, nF) for the 4 parental varieties and of the 6 selected plants with the greatest root size (A) and the 6 with the smallest (B) among their 12 mutual F_2 progeny grown at Hrubčice in 2011

Maternal variety	A plants	B plants	Paternal variety
Prestige 8.08	10.90	3.02	Saloon 8.59
	12.56	3.78	Jersey 9.21
	13.20	4.81	Diplom 8.57
Saloon 8.59	9.43	4.30	Prestige 8.08
	10.64	5.76	Jersey 9.21
	11.90	5.40	Diplom 8.57
Jersey 9.21	14.20	5.52	Prestige 8.08
	12.20	4.58	Saloon 8.59
	12.93	6.01	Diplom 8.57
Diplom 8.57	10.76	5.46	Prestige 8.08
	10.98	5.43	Saloon 8.59
	14.68	4.72	Jersey 9.21
Average 8.61	12.03	4.90	8.61

The selection A plants had a larger root system than either of their parents in all 12 combinations, whereas the selection B plants had a smaller root system than either of their parents in all 12 combinations. The average size for all parents was 8.61 nF, while the average for all selection A plants was 12.03 nF (39.7 % larger than the average for the parents), and the average for all selection B plants was 4.90 nF (43.1 % smaller than the average for their parents). The differences between selection A, selection B, and parental plants were mutually not significantly different.

We evaluated three of the four varieties in a previous paper (Chloupek et al. 2010). The Prestige variety exhibited a small average root system size over the four experimental years, including in the dry year of 2007, as did its progeny, which are shown in Table 2. Two other varieties responded differently in different years in terms of both root system size and grain yield. Diplom had a large average root system size over the four examined years, but a smaller size in the dry year; in the present study, the progeny of this variety inherited genes for large root systems.

The general combining ability is the ability to obtain higher values than the average of all combinations, calculated from both reciprocal crosses. The average root system size for the selection A plants from all 12 combinations was 5.03 nF, and that in selection B was 4.73 nF (in bold in Table 2; the average value of the parents is in italics). For example, the effect of the general combining ability for the Prestige plants in selection A was (5.35+4.27)/2−5.03=−0.22 nF, and that in selection B was (5.36+4.00)/2−4.73=−0.05 nF.

Comparison of the average values recorded for the four parental varieties in 2011 and 2012 (first column in Table 1 and last row in Table 2) showed a correlation of r^2=0.499. The

Table 2 Root system sizes (sum of three measurements, nF) for the 12 F_3 populations selected for large roots (A) or small roots (B) and the averages for the parents (C) at Hrubčice in 2012

♀/♂		Prestige	Saloon	Jersey	Diplom	Average	Effects of the general combining ability
Prestige	A	–	6.14	5.22	4.69	5.35	−0.22
	B		6.04	4.70	5.34	5.36	−0.05
	C		5.32	5.49	4.27	5.03	–
Saloon	A	4.75	–	5.60	5.19	5.18	+0.40
	B	4.83		5.06	4.41	4.77	+0.17
	C	5.33		4.09	5.39	4.94	–
Jersey	A	1.83	4.40	–	4.47	3.57	−0.54
	B	1.81	4.57		5.62	4.00	−0.35
	C	1.77	5.29		5.33	4.13	–
Diplom	A	6.22	6.48	5.41	–	6.04	+0.38
	B	5.36	4.51	4.50		4.79	+0.23
	C	4.99	5.19	5.57		5.25	–
Average	A	4.27	5.67	5.41	4.78	**5.03**	0
	B	4.00	5.04	4.75	5.12	**4.73**	0
	C	4.03	5.27	5.05	5.00	*4.84*	–

average values for the 12 progeny of the 6 plants showing the greatest root system size from each combination selected from 24 plants corresponded to a 3.9 % greater root system size than the average observed for all parents in the same year.

The average root system size of the 12 populations included in selection A was 5.03 nF, whereas in selection B, it was only 4.73 nF (6 % less). The greatest root system sizes were found in the progeny of Diplom × Saloon, Diplom × Prestige, and Prestige × Saloon crosses (6.48, 6.22, and 6.14 nF, respectively). The smallest root system size was found in the progeny of the Jersey × Prestige cross (1.81 nF). Evaluation of the general combining ability (last column in Table 2) showed that the use of Saloon and Diplom parents led to an increased root system size in both selection A and selection B and that crosses involving Prestige and Jersey had a smaller root system size in both selections.

The grain yields of the parents and of all their progeny were similarly evaluated (Table 3).

The average grain yield obtained for the 12 progeny of the 6 plants with the greatest root system size among the 24 plants for each combination was 8.1 % higher than the average for all parents in the same year. In other words, plants with a 3.9 % larger root system size showed an 8.1 % higher yield (e.g., sizes of 4.84 and 5.03 nF and yields of 6.67 and 7.21 g for the parents and their progeny). Similarly, selection B, including the progeny with the smallest root system sizes (2.3 % smaller),

Table 3 Grain yield per plant (gram) for the 12 F_3 populations selected for a large (A) or small root size (B) and the average of the parents (C) at Hrubčice 2012

♀/♂		Prestige	Saloon	Jersey	Diplom	Average	Effects of the general combining ability
Prestige	A	–	7.20	6.90	9.90	8.00	+0.55
	B		9.16	7.25	8.79	8.40	+0.90
	C		7.80	7.53	5.36	6.90	–
Saloon	A	7.46	–	8.80	4.58	6.95	+0.06
	B	5.74		6.54	4.29	5.52	−0.46
	C	8.66		5.60	5.36	6.54	–
Jersey	A	4.95	7.45	–	5.41	5.94	−0.70
	B	4.48	6.44		6.54	5.82	−0.17
	C	7.98	6.72		6.73	7.14	–
Diplom	A	10.18	8.16	5.56	–	7.97	+0.09
	B	7.94	3.04	5.72		5.57	−0.28
	C	5.50	6.85	5.92		6.09	–
Average	A	7.53	7.60	7.09	6.63	**7.21**	0
	B	6.05	6.21	6.50	6.54	**6.33**	0
	C	7.38	7.12	6.35	5.82	*6.67*	–

was characterized by a 5.1 % lower yield, which is also a yield effect of approximately twice the difference in root system size, similar to selection A.

The relationship between the root system size and grain yield in the selection A and selection B populations is presented in Fig. 2. It can be seen in Fig. 2 that larger root systems were related to higher yield; in selection A, the correlation was r^2=0.225, while in selection B, the correlation was higher and significant (r^2=0.396; p value=0.05). Plants with small roots systems (selection B) had greater grain yield per unit of root increment; that is, each nF of root system size was related to 2.59 g of grain yielded from the plant, since the overall root system size was 4.99 nF. In selection A, the average root system size was 5.32 nF and each nF corresponded to only 0.74 g of grain. Therefore, there was a higher grain yield per unit increment of roots in populations with small root systems.

Drought-induced losses in crop yields most likely exceed losses from all other causes because both the severity and the duration of the stress are critical (Farooq et al. 2009). Rapid and accurate phenotyping remains the major bottleneck to enhancing yield gains in water-limited environments. For most traits that are important in dry environments, selection is generally conducted most effectively in environments with favorable moisture (Richards et al. 2010). Drought has been shown to induce larger diameters in two wheat species (Ebrahimi et al., unpublished data), with one of these species investing more assimilates into its roots, while the other reduces its leaf area and numbers of fine roots.

The method employed for the evaluation of root system size enabled effective selection for this trait, which was performed under favorable conditions. Cultivar diversification can potentially increase the mean regional yields of feed barley. Increasing cultivar diversity therefore offers a novel,

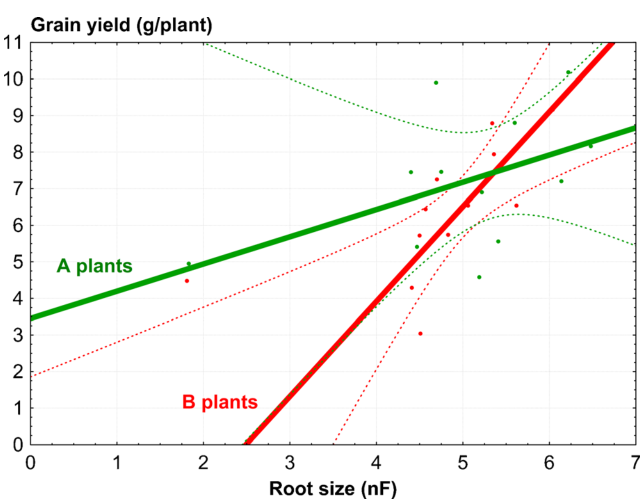

Fig. 2 Relationship between root system size and grain yield in selection A and selection B plants. Scatterplot with regression lines and 95 % confidence bands. Only 11 averages of 6 plants were evaluated since 1 plant in selection A and 1 in selection B had an outlying average

sustainable method for promoting higher yields (Himanen et al. 2012), particularly in the context of frequently occurring droughts. There is a need for tools for the evaluation of cultivars that include both the environmental characterization of trials and advanced statistical analysis of genotype by environment interactions (Lecomte et al. 2010). Our research meets the suggested requirements by enabling greater diversification through selecting for a larger root system. In the dry year of 2007, the root system size of winter wheat was influenced most by the location (83–86 % of the total variation) followed by the variety (8–10 %). The interaction between the varieties and their locations was significant only during heading, when this relationship explained 4 % of the observed variation (Středa et al. 2012). In spring barley, the highest percentage of the total observed variation was also explained (Chloupek et al. 2010) by the location (42–88 %), followed by the variety (3–16 %) and by unexplained variation (2–8 %). Similar values for genetic variability were identified in extensive official variety trials examining spring barley grain yields in Germany, with the greatest effects found for location (8.3 %), variety (3.5 %), and error (4.9 %), as reported by Laidig et al. (2008). This report describes the relationship between root system size and grain yield during selection for large or small root systems, where it was found that a 1 % change in root system size corresponded to a 2 % change in yield.

3.3 Response to selection

The average response to selection can be calculated as a comparison of the difference related to selection in the F_2 generation with the realized difference in the F_3 progeny. These values can be regarded as the realized heritability of the trait. We found that the average selection difference in selection A was +39.7 % and the change in the progeny was +3.9 %, while in selection B, these values were −43.1 and −2.3 %, respectively. Only 9.8 % (3.9/39.7) of the selection-associated difference in the F_2 plants was realized in the F_3 progeny in selection A and only 5.3 % (−2.3/−43.1) in selection B. These results suggest that the examined trait is controlled by many genes, as suggested for barley by Chloupek et al. (2006). The response to selection for root system size, measured by electrical capacitance, was evaluated previously in two alfalfa cultivars for 3 years. Plants with a root system size that was significantly larger or smaller than the cultivar mean were selected, and their open-pollinated progeny were evaluated over the following 3 years. The progeny of plants with a large root system tended to exhibit larger root systems and a higher forage yield than the progeny of plants with a small root system (Chloupek et al. 1999). The differences in both parameters were significant in the case of the variety *Zuzana*, which was developed by including one of five clones with significant effects for the general combining ability for root system size (Chloupek 1982).

Richards and Passioura (1989) undertook a backcross breeding program using two commercial Australian varieties that were crossed with a Turkish landrace to reduce the xylem vessel diameter of derivatives from about 65 to 55 μm. In field trials conducted over 5 years, selections with narrow vessels yielded between 3 and 11 % more than the unselected controls. This project was at the time the only one for which a cereal crop had been specifically bred for a root character (Gregory 2006).

Messmer et al. (2011) reported a heritability of root capacitance in maize of close to 0.5 under three different water regimes. The correspondence of quantitative trait loci between root traits measured at the seedling and flowering stages is encouraging for the development of methods that allow the investigation of root systems at early stages, with the objective of predicting the drought resistance of maize genotypes. We found that selection A resulted in a greater response than selection B. This finding can be explained by evolutionary advantages, as previous selection efforts were mostly directed towards grain yields, grain quality, and resistance, rather than root system size, which can represent a bottleneck for grain yields.

In a previous study (Chloupek et al. 2010), we evaluated the relationship between the root system sizes and yields of approximately 20 barley varieties over the course of 5 years in official variety trials. Only the dry year of 2007 resulted in varieties with a larger root system and a higher yield of better quality grain. Another such dry year occurred in 2012, during which we observed a significant correlation between root system size and grain yield, as shown above. This result indicates that, over eight evaluated years, a larger root system was only advantageous in 2 years. However, in some locations, the relationship between root system size and yield was also negative, as shown in winter wheat (Středa et al. 2012). We therefore propose that approximately one fourth of barley acreage should be made available to varieties with larger root systems in central Europe.

4 Conclusion

We show here that the size of the root system was related to grain yield in barley and selection for the trait was effective. About 10 % of the selection difference in parental generations was inherited into progeny when selecting for larger root systems and about 5 % when selecting for smaller root systems. In both selections, the change in grain yield was twice the change in root system size. The response was higher in populations with smaller root systems. Such a selection was made possible by using electrical capacitance measurements. In this way, plant breeding could contribute to resolving problems associated with shortages of water for cereal cultivation.

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