

Direct effects of cyclic selection for longer seminal roots in spring barley (*Hordeum vulgare* L.)

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Abstract. Cyclic pedigree selection for longer seminal roots was performed in the F₂, F₃ and F₄ generations of hybrid population of spring barley. The total length of roots was measured in seedlings grown in filter-paper rollers. The intensity of selection was 20% (C₁, C₂ cycles) and 26% (C₃). Selection was effective. On an average, the finally selected F₅-pedigrees formed 6% longer seminal root system than the initial F₂'s and much of them exhibited 7-16% improved rooting when compared with the best parent in a sand-vermiculite pot culture. Realized heritability coefficient of the root length ranged from 0.21 to 0.37 when assessed by the ratio of selection response to selection differential, while those estimated by the parent-offspring regressions attained 0.40-0.53. The obtained results suggest that progeny evaluation and/or selection delayed for later generations should be essential for more effective root selection in barley.

Key words: *Hordeum vulgare* L., realized heritability, root length, selection, seminal roots.

Root characters have been already recommended many times for cereal selection. However, few results have been hitherto published to prove such an effective use of root criteria in wheat and oat breeding (KIRICHENKO et al. 1968, HURD 1974, LARSSON, STOY 1982, BARBOUR, MURPHY 1984, RICHARDS 1987). Cereal breeders are still sceptic. Besides methodical questions, there is an extremely limited knowledge on root inheritance due to a slow progress in genetic studies on roots (rev. by TROUGHTON, WHITTINGTON 1969, O'TOOLE, BLAND 1987, CHLOUPEK, ROD 1992).

There are various reasons for which the use of juvenile root criteria in cereal selection would be justified. The most important appear to be possible asso-

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ciations of the juvenile root growth with seedling emergence, their competition ability, nutrients efficiency, field plant establishment and yield potential, in consequence. The relationships could be especially expected on light-textured podzolic soils where water and/or nutrients imbalancies may contribute to a considerable depression in plant performance.

Results of preliminary studies in oat and spring barley suggested that improving selection should be more effective for juvenile (i.e. seminal) than for adventitious root characters (GÓRNY 1992). The former, indicating higher heritabilities, appeared to be more suitable for genetic alterations. Therefore, a cyclic selection for longer seminal roots was conducted in a hybrid population of spring barley to evaluate its direct effects and realized heritability of the total length of seminal roots in seedlings.

Material and methods

Plant materials and laboratory experimental procedure

The F₂-generation of a hybrids between the Polish cv. Dema and Dutch cv. Apex of spring barley constituted the initial population, in which a 3-cycle selection for longer seminal roots was begun. The parental cultivars were chosen to be representative of different yield potentials and cultivation requirements. The cv. Dema required markedly higher inputs than the cv. Apex.

Attempts were made to choose a method non-destructive for measured plant materials. The method should permit a screening of large number of plants. Thus, seedlings were grown in 30 cm long filter-paper rollers as described elsewhere (GÓRNY, GEIGER 1982, GÓRNY 1992). Surface-sterilized (5% sodium hypochlorite) and pre-soaked (2 h, water) seeds were germinated on wet filter paper for 14-16 h at 20-22°C. To eliminate possible effects of endosperm size, only seeds of a uniform fraction were used. The average grain weight ranged from 42.5±2 mg, through 44±3 mg and 46±3 mg to 47±3 mg in the C₀, C₁, C₃ and C₂ selection cycles, respectively. Pre-germinated seeds (emerged primary root was 0.5-1 mm long) were sown embryo-down in rollers which contained plastic-coated iron wires for air exchange. Packets of the rollers were vertically placed in a shallow distilled water bath and kept in a growth chamber under illumination of 9.000-10.000 Lx, 16 h photoperiode and controlled maximal and minimal temperatures. They were maintained at 23/18°C day/night. The roller-packets were rotated around the experimental area everyday to minimize the effects of possible light intensity or temperature gradients. A selected character was the total length of seminal roots. The length of all

roots was measured in seedlings at the beginning of the 2-leaf stage (11 days after sowing pre-germinated seeds). After the measurements, the selected F_2 -seedlings (C_0 -cycle) or seedlings of pedigrees selected in the C_1 and C_2 cycles were transplanted into soil pots for further propagation under greenhouse conditions. Using the same procedure, parents and their F_1 -hybrids were simultaneously propagated in the pots.

Considering recommendations made by plant physiologists (e.g. HEYDECKER 1977, GRZESIUK, KULKA 1981), a strong care was taken during the whole experiment to decrease experimental error and enhance operative heritability of the selected root character by a control of possible effects of factors expected to have an influence on seedling growth.

Experimental designs and selection

Mass selection (in the F_2) and pedigree selection (in later generations) for the longest seminal root system were performed with an intensity of about 20% at the each selection cycle, except for the F_4 -generation (C_3 -cycle) where, depending on a more narrow genotypic variation and estimated LSD-values, a possibly low intensity was established at about 26%.

In the C_0 -cycle, a total of 1354 plants of the initial F_2 -generation was grown in 45 rollers (30-32 plants per a roller) and these were compared with both parental lines represented by 90 plants (3 replications with 30 plants). In each roller with F_2 's, about 20% seedlings with the longest root system were selected and transplanted into soil pots (greenhouse) to obtain 271 F_3 -progenies. In the C_1 -cycle, the selected 271 F_3 -pedigrees, both parents and F_2 -generation were evaluated in a 3-times replicated experiment with 30 (parents and F_2 's) and 6 seedlings (F_3 's) per each replication. Similar design was used in the C_2 -selection cycle with 54 F_4 -pedigrees. In the C_3 -cycle, the finally selected 14 pedigrees of the F_5 -generation were compared with their parents and the initial F_2 -population in the 2-times repeated experiment performed with three replications and 16 seedlings per replication. All the experiments were arranged as randomized designs with genotypes splitted over replications.

Evaluation of selected F_5 -pedigrees in a pot experiment

The selected 14 pedigrees of the F_5 -generation were compared with the parental lines and F_2 -generation in a greenhouse experiment using a procedure described elsewhere (GÓRNY 1994). Plants were grown in drained PVC cylinders (50 cm deep, diameter 7.5 cm) filled with a mechanically prepared pure quartz sand : vermiculite (3:1, v/v) mixture initially moistened with 350 ml of a nutrient solution. Ten uniform, surface-sterilized and pre-germinated seeds

were sown per each tube-replication. The 16/8 h day/night cycle and supplementary light (9.000 Lx) were used. The maximal and minimal temperatures were maintained at 21/10°C day/night. To minimize eventual effects of light and temperature gradients, covered packets of cylinders were placed in drained containers and everyday displaced around the experimental area. A modified basal Long Ashton-nutrient solution was added onto the growth medium surface. Cylinders received 100 ml of the solution every two days and 50 ml distilled water in residual days. The experiment was performed with three replications. All plants were harvested four weeks after sowing pre-germinated seeds. Roots were gently separated by washing. The total root length was measured by the line intersection method using the Delta-T Image Analysis System (Delta-T Devices Ltd., Cambridge, U.K.). Dry matter (DM) of shoots and roots was determined after oven drying at 65°C for 48 h.

Statistics

The standard MSTAT-C package was used for most statistic data computations. In the C_0 -cycle, parental means were compared with F_2 -mean by LSD-values as calculated after the analysis of variance (ANOVA). In residual cycles, comparisons between respective groups of materials were made by F -tested contrasts (KACZMAREK 1994). Realized heritability was calculated in two standard ways, as the ratio of selection response to selection differential and as the b coefficient of the parent-offspring regression (FALCONER 1981).

Results

Mean total lengths of seedling roots in parents, initial F_2 -population and in the F_3 , F_4 and F_5 pedigrees selected in three selection cycles are presented in Table 1. The total root length of the progenies obtained in the C_1 , C_2 and C_3 cycles was enhanced as compared with the initial F_2 -population. The relative changes in the root length were partly dependent on the selection cycles and homogeneity of materials, and those for the F_4 (C_2 -cycle) and F_5 (C_3 -cycle) pedigrees were found to be significant. There was rather a curvilinear response to selection, and the progress appeared to be partly established already in the C_1 -cycle. The root length enhanced by 4.8% in the first cycle, and finally the selected F_5 -pedigrees ($n=14$) formed, on an average, about 6% longer juvenile roots than the initial hybrid population.

The estimated realized heritabilities of the total root length were low or moderately low ranging from 0.21-0.37 to 0.40-0.53 when estimated by stand-

Table 1. Heritability coefficients and means for total length of seminal roots in parental lines (cvs. Dema, Apex), initial F₂-population and in selected pedigrees of respective selection cycles

Selection cycle	Total length of seminal roots (cm)				Heritability coefficients		
	cv. Dema	cv. Apex	F ₂	Selected pedigrees (F _n)	R/S	$b_{F_n/F_{n-1}}$	h^2
C ₀	123.9*	112.6	118.1	—	—	—	0.518
C ₁	115.7*	106.9	109.8	(F ₃) 115.1	0.211	0.402	0.630
C ₂	132.5*	119.2	125.7	(F ₄) 130.5*	0.256	0.533	0.691
C ₃	132.9	120.8*	128.2	(F ₅) 135.9**	0.367	0.415	0.786

*,** significantly different from F₂-means at the P=0.05 and P=0.01 levels, respectively.

ard R/S ratio and by parent-offspring regression, respectively. The broad-sense heritability values, as calculated using variance components by ANOVA, ranged from 0.52 in the F₂ to 0.79 in the final F₅-generation.

On an average, the performed selection for longer roots did not contribute to significant correlated alterations in residual shoot and root characteristics (Table 2). Generally, such changes did not occur under laboratory and greenhouse conditions. All considerable differences between F₂ and F₅ means concerned only the root length. No such differentiation was also found for the root dry matter in a greenhouse-pot experiment, although F₅-selections tended to form finer roots.

When considered individually under laboratory conditions, nine F₅-lines formed significantly longer roots than the F₂'s, but only four of them exhibited about 5-8% more vigorous rooting than their best parent (cv. Dema). At the later growth stage (just before the tiller formation) in the pot experiment, eight F₅-selections were found to develop by 7-16% longer roots than the cv. Dema and F₂'s (Table 2).

As shown in Table 3, the genotypes at the 2-leaf stage were found to have a significant correlation ($r = 0.75$, $P < 0.01$) between the total length and number of seminal roots. No considerable relation ($r = 0.33$, $P > 0.10$) was found between the total root length and the longest root length. Some positive, but non-significant relations occurred also between residual shoot and root parameters at the growth stage. The correlation coefficient between the total root length measured in filter-paper rollers and that in pots was $r = 0.54$ ($P < 0.05$) indicating a consistence between the root length characteristics measured under

Table 2. Morphological shoot and root characters of the selected F₅-pedigrees as compared to their parental lines and initial F₂-generation in laboratory and greenhouse-pot experiments

Genotype	2-leaf stage (filter-paper rollers)				4-leaf stage (sand-vermiculite pots)				
	1st leaf length	total root length	longest root length	No. of main roots	shoot dry matter (S)	root dry matter (R)	S : R ratio	total root length	root fineness
	(cm)	(cm/plant)	(cm)		(mg/plant)			(cm/plant)	(mg/m)
cv.DEMA	16.0	132.9	28.2	6.7	48.9	12.0	4.1	189.5	6.3
cv.APEX	14.7	120.8	27.0	6.4	45.9	12.6	3.7	185.7	6.9
F ₂	14.7	128.2	27.3	6.7	46.2	12.0	3.9	190.1	6.4
F ₅ -pedigrees:									
L. 29	14.9	144.0	28.0	7.2	46.6	12.6	3.7	208.7	6.0
L. 33	15.4	141.1	28.2	7.0	44.5	13.7	3.3	213.2	6.5
L. 54	14.7	139.4	27.6	7.0	46.7	12.6	3.7	219.0	5.8
L. 38	14.7	139.3	27.5	7.0	48.2	13.2	3.7	210.1	6.3
L. 13	15.0	136.6	28.3	6.6	47.4	11.6	4.1	190.1	6.1
L. 23	15.1	136.7	27.4	7.1	49.4	12.9	3.9	211.1	6.1
L. 7	15.8	136.3	29.0	6.6	49.7	12.1	4.1	202.6	6.0
L. 10	16.1	136.4	27.2	7.1	49.2	13.1	3.8	201.3	6.6
L. 52	15.8	136.0	28.2	6.8	42.3	11.3	3.7	191.6	6.0
L. 22	15.6	133.5	28.1	6.7	42.9	11.5	3.7	215.1	5.4
L. 6	15.2	133.3	27.9	6.7	49.3	11.9	4.2	189.7	6.3
L. 18	15.2	131.7	27.8	6.6	46.2	13.6	3.4	220.3	6.2
L. 51	14.6	130.8	26.8	7.0	38.2	9.7	3.9	173.6	5.6
L. 17	14.3	128.1	28.4	6.4	39.8	11.7	3.4	177.5	6.6
<i>LSD</i> _{0.05}	0.8	5.9	1.1	0.3	4.1	1.0	0.4	11.7	0.6
F ₅ -mean	15.2	135.9	27.9	6.8	45.8	12.3	3.8	201.7	6.1

laboratory and greenhouse conditions at the 2-leaf and 4-leaf growth stages, respectively. As expected, positive associations were observed between shoot and root dry matters as well as between the total length and root DM of genotypes grown in the pot experiment.

Table 3. Correlation coefficients between shoot and root morphological characters estimated in laboratory and greenhouse-pot experiments

Trait	2-leaf stage				4-leaf stage		
	1st leaf length (1)	total root length (2)	longest root length (3)	root number (4)	shoot dry matter (5)	root dry matter (6)	total root length (7)
(1)	–	0.27	0.36	0.11	0.39	0.17	0.26
(2)		–	0.33	0.75**	0.30	0.19	0.54*
(3)			–	–0.32	0.12	0.02	0.13
(4)				–	0.20	0.11	0.39
(5)					–	0.57*	0.41
(6)						–	0.69**

*,** -significant at the P=0.05 and P=0.01, respectively

Discussion

The obtained results show that selection for longer seminal roots at the seedling stage may contribute to considerable genetic alterations in variation range of the character in spring barley. On the average, the selected F₅-pedigrees formed about 6% longer seminal root systems than the initial F₂-generation. Many of them, exhibiting a transgressive segregation, have a considerably improved (by 7-16%) rooting capacity when compared with their best parent in a pot experiment. The averaged selection gain was about 2.6 cm root length per cycle, although the response was not exactly linear; the gain tended to establish after the first selection cycle suggesting that relatively few major genetic factors were involved in the control of root length of the cross population. The mean 6% response appears to be rather comparable to the magnitude of responses reported for many quantitative plant characters. Partly similar response to selection for longest root length was previously reported by BARBOUR and MURPHY (1984) in *Avena sativa* grown in a modified Hoagland's solution.

It appears that selection for longer juvenile roots may be effective in barley, but depending on genetic mechanisms involved that may be relatively difficult to perform. The estimated heritability values indicating significant effects of additive genes on the genetic variation of the root length were, however, found to be low or lowly moderate (0.21-0.37 to 0.40-0.53). Because of a lack of data on inheritance of the selected character as assessed in typical cross

experiments (e.g. diallel crosses) with parents used in the present study, it is difficult to generalize with regard to the inheritance patterns responsible for the root length. Comparing our previous data (GÓRNY 1992), it appears that mechanisms involved in the inheritance of the character seem to vary due to different genetic constitution of parents. Nevertheless, the lower realized heritabilities may suggest that non-additive gene effects should also be considered when assessing a possible selection gain for the root length in barley cross populations. Hence, the progeny evaluation and selection as delayed for later generations may be proposed for likely more effective root selection and/or progeny evaluation in spring barley.

On the other hand, the operative heritability values, as estimated in the F_{2-5} using variance components by ANOVA, were higher (0.52-0.79) indicating that the total root length was under a relatively low pressure of environmental conditions in this study. It should however, be mentioned that the applied procedure was laborious and needed a high accuracy. During the whole experiments a strong care was taken to decrease the experimental error and to enhance the operative h^2 . This may have some implications in breeding practice. Obviously, numerous non-genetic factors may have an influence on the expression of the root length. After our experience, care for a proper control of experimental conditions and procedural accuracy should only lead to a satisfied progress.

Probably due to methodical questions, in numerous reports the so-called root length in seedlings is estimated only by measuring the length of the longest root. In the present study, however, there was a non-significant correlation between the length of longest root and the total length of roots. This suggests that the length of longest root may not be a totally adequate predictor of the whole root system size.

A stronger correlation occurred between the total root length and the number of main roots. It seems that in the studied population the root number was a more important contributor to the size of the whole seminal root system than the longest root length. Therefore, genotypes selected for an enhanced root number may be expected to have an adaptive advantage, as previously suggested by MAC KEY 1979, ROBERTSON et al. 1979, PFAHLER et al. 1987 and others. However, the efficiency of selection based only on the root number should be carefully assessed. As shown other reports, the above-mentioned close relation between the number and whole length of juvenile roots did not appear to be a rule in cereals. Moreover, the number of seminal roots appears to be of various inheritance pattern, and there are available data showing its

relatively low heritability (VERMA, NAGI 1974, RICHARDS, PASSIOURA 1981, GÓRNY, GEIGER 1982, GÓRNY 1992).

Generally, results of the study indicating a possibility to spread the variation in juvenile rooting by selection may be suggestive that the obtained progenies will exhibit an improved adaptability to unfavourable environments. Further research on selected lines under water and mineral limitations is essential for more precise assessment of their performance in less favourable conditions.

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