IJBPAS, March, 2015, 4(3): 1127-1134

ISSN: 2277–4998

International Journal of Biology, Pharmacy and Allied Sciences (IJBPAS)

'A Bridge Between Laboratory and Reader'

www.ijbpas.com

HERITABILITY OF ROOT CHARACTERS OF BARELY CULTIVARS UNDER DROUGHT STRESS

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ABSTRACT

To evaluate the inheritance of root characters of barely cultivars under drought stress, the F_1 seeds of a 6×6 half diallel, along with their parents were grown in greenhouse in randomized complete block design with three replications. After growing and maturity, root traits such as root main branches, root length, root dry weight was measured. The experiment was carried out at Islamic Azad University, Ardebil, Iran in 2014. Results showed that additive-dominant model was adequate for determining the inheritance of the traits. All of the traits had high broad sense heritability; however among the traits root main branches had moderate narrow scenes heritability and other two traits had relatively low narrow sense heritability. All of the traits governed with over dominance, while the magnitude of average degree of dominance was greater in root dry weight. Higher frequency of dominant alleles in the parents was also demonstrated in all of the traits. Dominant alleles were favorable in root length and dry weight, however such relation was not observed in case of root main branches. The significant GCA mean square suggests that genetic gain is achievable through selection over the segregant population. However, due to high average degree of dominance, selecting for drought tolerance must be done in advanced generations of wheat breeding programs. Results of combining ability analysis also showed that under drought stress, genotype number 6 had favorable additive genes for root length, while genotypes number 4, 5 and 6 had good gens for root main branchs.

Keywords: Root Characters, Diallel, Drought, Heritability, Barely

INTRODUCTION

Drought is a major abiotic stress, limiting crop production in arid and semi-arid climates. Stress resistance in plants is a complex character that depends on many genes and thus is determined by the interactions of many morphological, physiological and biochemical processes. Root architecture is an important regulator of water acquisition under drought. Plants with longer and deeper roots have better access to water resources available at depth, and are therefore more prevalent among species found in dry environments **(Merrill *et al*., 2002; Ho *et al*., 2005; Moroke *et al*., 2005; Morison *et al*., 2008)**. The physical location of roots is clearly important because roots are the pathways of water uptake, and traits that optimize the co-location of roots with available water resources will increase water acquisition **(Lynch, 2007a, b; Ho *et al*., 2004; Benjamin and Nielsen, 2006; Songsri *et al*., 2008)**. Root characteristics can be measured relatively easily, so potentially can be considered as selection criteria if they also have high heritability. The objective of this study was determination of the inheritance of some root characteristics in barely cultivars.

MATERIALS AND METHODS

Six barely varieties **(Table 1)** were crossed in half diallel fashion. The F1 seeds, along with their parents were grown in greenhouse under well watered drought stress conditions using randomized complete block design with three replications at Islamic Azad University, Ardabil, Iran in 2014. Seeds of the genotypes were sown in 10cm diameter and 100cm long polyvinyl chloride (PVC) tubes filled with 10 kg of soil composed of a mixture of soil, compost and sand (1:1:1, v/v). Two drainage holes made at the bottom of each bag were covered with a filter paper before being filled. Throughout the study, tubes of well watered condition were always maintained in field capacity, tubes of stress conditions were maintained in 50% of field capacity. Measured root parameters included root length, root dry weight and root volume. To measure root dry matter the roots were dried at 70°C and weighted after 24 h.

Statistical analysis

The detailed analysis was done according to the theoretical basis developed by **Hayman (1954a),** adapted for the half diallel by **Walters and Morton (1978)**. The goodness of fit of the additive-dominant model was performed based on the analysis of variance of Wr-Vr and linear regression of Wr on Vr **(Hayman, 1954a)**. The genetic components: D, H1, H2, F and h2 were estimated according to Singh and Singh (1984). Standard errors of these components were calculated from expected and observed values of Wr, Vr, $\bar{Vr}$,Vp and (mL1- mL0)2 over replications **(Hayman, 1954a)**. From the estimates of the genetic components, the genetic parameters presented in Table 4 were estimated. Average degree of dominance, broad sense heritability and narrow sense heritability were calculated according to **Mather and Jinks (1971)**. Combining ability analysis was also carried out following Model I and Method II of **Griffing (1956)**. Following **Baker (1978)**, the variance ratio 2S2gca/2S2gca+S2sca was computed from expected components of mean squares assuming a fixed model, to assess the relative importance of additive and non-additive gene effects. Analysis of variance of Diallel was performed using the DIAL98 software **(Ukai, 1989)**, genetic components were estimated by electronic spreadsheets in the Excel program (Microsoft® Excel 2010). Combining ability analysis was performed using SAS 9.2 Software.

RESULTS

The results of the goodness of fit of the additive-dominant model are shown in **Table 2**. Non-significant Wr-Vr mean squares for treatment (crosses) indicated the adequacy of additive dominant model for the traits. The slops of linear regression were also significantly higher than zero and did not show significant differences with 1 **(Table 2)**.

The Analysis of variance of the diallel is shown in **Table 3**. Additive variance (a component) was highly significant in all of traits indicating the presence of additive effects in their control. The significance of (a) in **Table 3** was in accordance with the significance of additive effects (D component) in **Table 4**. The dominant genetic effects (b source of variation) showed highly significant effects in root branches and root dry weight (under stress), indicating the importance of dominant genetic effects in these traits. The "b1" component which measures the mean deviations of the F1s from the mid-parental values was significant only in root length in non-stress condition **(Table 3)**. The significance of the "b1" component indicates that the dominance was predominantly in one direction and measures average heterosis **(Singh and Singh, 1984)**. Significance of b1 component was generally in accordance with higher magnitude of dominance ($\overline{F}_1 - \overline{P}$) where F_1s had lower root length than their parents. Since the mean dominance effect of the heterozygote locus (h^2) was significant only for root length and root branches (non-stress), high heterotic effect values would be expected for those traits among crosses **(Table 4)**. The "b2" component was significant only for root branches in non-stress conditions. The significance of the b2 item indicated that the mean dominance deviations of the F_1s from their mid parental values differed significantly over the F_1 arrays; this implies the presence of asymmetry in the distribution of alleles among the parents **(Hayman, 1954b)**. This also means that there was evidence that some parents had a significantly better performance than others (**Ramalho *et al*., 1993)**. Since b2 is significant for root branches in non-stress conditions, the 'a' item will not measure additive variance unambiguously, but it will be contaminated with non-additive variance also **(Singh and Singh, 1984; Chaudhary *et al*., 1977)**. The proportion of positive and negative genes was estimated by calculating (H2/4H1) in **Table 4**. This ratio was lower than 0.25 in all of the traits, indicating the presence of asymmetry in the distribution of the positive and negative alleles in the parents. This is also substantiated by H1 being greater than H2 in these traits. The "b3" component which is equivalent to specific combining ability variance was significant only in root branches. b3 estimates residual dominance effects combining from additive × additive, additive × dominance and dominance × dominance interaction effects that are not attributed to b1 and b2 **(Chaudhary *et al*., 1977)**. The estimate of the genetic component F was significant in root length and root branches (under stress) which is an indication of asymmetry in the distribution of dominant and recessive alleles in the parents. The ratio of the total number of dominant and recessive alleles in the parents (KD/KR) was higher than one in all of the traits, demonstrating a higher frequency of dominant alleles in the parents. Positive values for F substantiated by (KD/KR) being greater than one. The degree of average dominance was higher than one, indicating the presence of over dominance in control of traits. Over dominance also was confirmed by negative intercept of regression line (**Table 4**). Despite the high broad sense heritability (Hb) in all cases, Narrow sense heritability (Hn) of root branches was moderate and two other traits was relatively low (table4). The differences observed between the Hn and Hb reflected the presence of the dominant effects. In the study of **Edwards *et al* (1990)**, narrow sense heritability of root volume and root diameter in tall fescue was 0.41 and 0.18. Correlation coefficients between the parental means and order of dominance "rYr(Wr+Vr)" was negative in root length (non-stress) and root dry weight indicating that dominant alleles are favorable, however such relation was not clearly observed in other cases.

Combining ability analysis by Grifting's method indicated the significance of GCA mean squares. This shows the importance of additive effects **(Table 5)**. However SCA mean squares was significant in root length and root branches in non-stress condition. Higher Baker's ratio for traits suggests that additive effects are more important than non-additive effects in all cases **(Table 5)**.

The importance of GCA effects was also evident from the higher correlation between the parental means and the GCA effects in the case. Thus, the combining ability analysis was in good agreement with the conclusions from Hayman's method in showing the gene action in the inheritance of traits.

Table 1: List of cultivars used in the study

Cultivar	Pedigree/Origin
1	CWB117-77-9-7/4/Rhodes's'//Tb/checkzo/3/Gloria's'
2	U.N.K-80Kelar
3	Probesdwarf / Numar
4	Pamir-065/Sonata
5	Legia/3/LB.IRAN/UN8271//GLORIA
6	Rihane//Toji's'Robur

Table 2: Goodness of fit of additive-dominant model for evaluated traits

Character	environment	Heterogeneity of Wr-Vr (Mean squares)	t-test of b on the null-hypothesis	
			b=0	b=1
Root length	Non stress	264.3 ^{ns}	0.881**± 0.126	0.881^{ns}± 0.126
	stressed	291.1^{ns}	0.747**± 0.249	0.747^{ns}± 0.249
Root branches	Non stress	19.38^{ns}	0.794**± 0.203	0.794^{ns}± 0.203
	stressed	6.94^{ns}	0.911**± 0.289	0.911^{ns}± 0.289
Root dry weight	Non stress	0.0011^{ns}	0.649**± 0.119	0.649^{ns}± 0.119
	stressed	0.0009^{ns}	0.948**± 0.221	0.948^{ns}± 0.289

^{ns},* and ** non-significant and significant at the 5% and 1% levels, respectively

Table 3: Analysis of variance of the diallel tables for the evaluated traits

S.V.	d.f	Root length			Root branches			Root dry weight	
		Non-stress	stress		Non-stress	stress		Non-stress	stress
REP	2	8.6^{ns}	49.4^{ns}		5.57^{ns}	2.11^{ns}		0.13 ^{ns}	5.2**
a	5	235.7**	120.9**		120.9**	19.8**		0.24*	0.24**
b	15	51.8 ^{ns}	51.3 ^{ns}		73.5 **	11.2 *		0.13 ^{ns}	0.12 **
b1	1	210.3 *	0.16 ^{ns}		0.06 ^{ns}	0.06 ^{ns}		0.29 ^{ns}	0.22 ^{ns}
b2	5	59.04 ^{ns}	60.5 ^{ns}		73.5 **	4.5 ^{ns}		0.17 ^{ns}	0.13 ^{ns}
b3	9	30.2 ^{ns}	51.9 ^{ns}		81.7 **	16.1 **		0.09 ^{ns}	0.10 ^{ns}
Error	40	29.4	29.9		13.4	5.1		0.08	0.07

^{ns},* and ** non-significant and significant at the 5% and 1% levels, respectively

Table 4: Estimates of genetic components and related statistics in half- diallel design

	Root length		Root branches		Root dry weight	
	Non-stress	Stress	Non-stress	stress	Non-stress	stress
D	95.6**±2.9	48.9**±2.8	11.7**±1.1	46.6**±2.6	0.09 ^{ns} ±0.13	0.09 ^{ns} ±0.12
H_1	123.6**±7.2	107.4**±7.1	14.8**±2.8	12.9**±6.5	0.29 ^{ns} ±0.34	0.24 ** ±0.30
H_2	101.4**±6.5	86.0**±6.3	11.8**±2.5	69.6**±5.8	0.24 ^{ns} ±0.30	0.21 ^{ns} ±0.27
F	91.4**±6.9	44.1**±6.8	8.5 ^{ns} ±2.8	32.33**±6.3	0.08 ^{ns} ±0.32	0.06 ^{ns} ±0.29

h^2	**41.1**±4.4**	**14.8**±4.3**	**2.9**±1.7**	**4.31 ns±3.9**	**0.08 ns±0.20**	**0.06 ns±0.18**
E	**9.79 **±1.1**	**9.98**±1.1**	**1.69 **±0.42**	**4.45**±0.97**	**0.03 ns ±0.05**	**0.02 ns ±0.04**
Averag d	**1.14**	**1.44**	**1.12**	**1.40**	**1.81**	**1.62**
$H_2/4H_1$	**0.20**	**0.20**	**0.20**	**0.19**	**0.21**	**0.22**
KD/KR	**2.45**	**1.87**	**1.95**	**1.65**	**1.64**	**1.55**
Hn	**0.27**	**0.30**	**0.40**	**0.46**	**0.24**	**0.26**
Hb	**0.80**	**0.78**	**0.78**	**0.89**	**0.76**	**0.77**
rYr (Wr+Vr)	**-0.94 ****	**0.17 ns**	**0.51 ns**	**-0.28 ns**	**-0.78 ****	**-0.77 ****
$\overline{F}_1 - \overline{P}\%$	**-4.04**	**0.11**	**0.07**	**-0.07**	**0.15**	**0.13**
A	**-10.17**	**-13.35**	**-1.62**	**-8.69**	**-0.04**	**-0.05**

ns,* and ** non-significant and significant at the 5% and 1% levels, respectively

Table 5: Analysis of variance of the diallel tables for the evaluated traits

SOV	Df						
		Root length		Root branches		Root dry weight	
		Non-stress	stress	Non-stress	stress	Non-stress	stress
GCA	5	204.1**	109.1**	185.9**	32.7**	0.21**	0.25**
SCA	15	62.4*	55.2 ns	51.9 **	6.9 ns	0.14 ns	0.11 ns
Error	40	29.4	29.9	13.4	5.1	0.08	0.07
$\frac{2S^2_{GCA}}{2S^2_{GCA}+S^2_{SCA}}$	--	86.7%	79.8%	87.7%	90.4%	75.0%	81.9%

*** and ** significant at the 5% and 1% levels, respectively**

DISCUSSION

The fulfillment of assumption for Hayman's analysis indicated that a relatively simple genetic model was involved in the inheritance of traits. Since the degree of average dominance was higher than 1, the presence of over dominance and greater importance of dominance effects in control of traits was suggested. Regarding to the high broad sense heritability of traits under study, it can be concluded that they can be considered as candidates for selecting drought tolerance in barely. However relatively lower narrow sense heritability, suggests the use of multiple replications during selection to limit environmental effects. Regarding to the low narrow sense heritability of the traits, it can be concluded also that these traits can be considered as selecting criteria for drought tolerance in advanced generations of barely breeding programs. The significant GCA mean squares for traits indicated variability of GCA among the parents and this suggests that genetic gain is achievable through selection over the segregant population. In the combining ability analysis, additive × additive epistasis forms a specific part of variance due to gca, while epistasis of additive × dominance and dominance × dominance types are included in sca **(Griffing 1956)**. As additive gene action and additive × additive types of epistatic gene action are exploitable in homozygous genotypes, the estimates of gca effects of individual lines are a useful predictor for progeny performance in self-fertilizing species **(Baker1978)**. Finally, it is obvious that the two methods together provide more useful information on the mechanism of inheritance than each alone does.

ACKNOWLEDGMENT

Authors are very grateful to Islamic Azad University for financial support.

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