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Genetics and heritability of some physiological and agronomic traits in barley under drought stress

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Abstract
To evaluate the inheritance of some physiological and agronomic traits in barley, the F_1 seeds of a 5×5 half diallel cross, along with their parents were grown in well-watered and drought stress under greenhouse condition at the agricultural research station of Islamic Azad University, Ardabil, Iran in 2016. Physiological and agronomic traits such as relative water content, excised leaf water loss, stomatal conductance, cell membrane injury, chlorophyll fluorescence parameters, specific leaf area, leaf thickness, root length, root dry weight and grain yield were measured. Results showed that all traits had high broad sense heritability. Among the traits, cell membrane injury had the highest narrow sense heritability (0.47), followed by specific leaf area (0.369), excised leaf water loss (0.353) and relative water content (0.311). The average degree of dominance was higher than unity for all traits, indicating the presence of over-dominance gene action in the control of these traits. Results showed that for grain yield and specific leaf area, dominant alleles, and for cell membrane injury, recessive alleles are favorable. F1 progenies had lower specific leaf area, excised leaf water loss, relative water content, stomatal conductance and higher root dry weight than their parents. Due to the importance of dominance in the control of characters under study, it was suggested that the evaluation of traits under study should be done at advanced generations of inbreeding.

Keywords: Drought; Inheritance; Physiological traits; Root characteristics; Stomatal conductance

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Introduction

Drought is regarded as an important abiotic stress which limits crop production in arid and semi-arid regions. Many genes governs drought resistance in plants and thus this character is determined by the interactions of several morphological and physiological processes. Incorporation of physiological characteristics is regarded as an approach for development of cultivars for water-limited environments (Blum 2011). The selected traits for improving yield under water-limited conditions must be genetically correlated with yield, and its heritability should be higher than yield itself (Blum 2011). Furthermore, measurement of the target trait should be accurate, non-destructive, rapid and inexpensive (Tuberosa 2012). The success of any program for breeding drought-tolerant varieties depends on the precise estimates of genetic variance components for traits of interest. Hence, genetic designs such as diallel cross can be useful in providing information about the genetics of traits in the segregating generations. Physiological traits such as relative water content (Boyer *et al*. 2008), chlorophyll fluorescence parameters (Sayar 2008), stomatal conductance (Jiang *et al*. 2006), cell membrane stability (Sayar *et al.* 2008), specific leaf area (Vile *et al.* 2005) and root characteristics (Craine *et al.* 2002), are proposed as selection criteria for screening drought tolerance in crop plants. But little work has been done on the genetic behavior of these traits in barley and most of the work has been done on agronomic traits. For most of the agronomic traits, estimate of narrow sense heritability was high (Mohammadi *et al*., 2006; Jalata *et al*., 2011; Ebadi-Segherloo, *et al*. 2016), however for physiological traits, similar studies are scarce. Marcial and Sarrafi (1996) reported that chlorophyll fluorescence parameters in barley are mostly under the control of additive genetic effects.

The objective of this study was to evaluate the inheritance of several physiological and agronomic traits in barley under well-watered and drought stress conditions.

Materials and Methods

Plant material and experimental design

Five drought tolerant and susceptible barley advanced lines (Table 1) which were obtained from Seed and Plant Improvement Institute of Iran, were crossed in a half-diallel pattern. The F_1 seeds, along with their parents were grown in greenhouse under well-watered and drought conditions using randomized complete block design with three replications at the experimental field of Islamic Azad University, Ardabil, Iran in 2016 growing season.

Table 1. List of advanced lines of barley used as diallel cross parents in the study

Parent	Pedigree of advanced line	Drought tolerance
1	(CB74-2)CWB117-5-9-5	Susceptible
2	Astrix(c)/3/Mal/OWB753328-5H'F1//perge/Boyer/4/l.527	Tolerant
3	Robur/80-5151//cwb117-5-9-5	Tolerant
4	H177-02	Susceptible
5	Courlis/Rhn-03	Semi-tolerant

Growth condition

Five seeds were grown in polyvinylchloride tubes with 100 cm depth and 25 cm diameter, filled with 15 kg of soil composed of a mixture of garden soil, vermicompost and sand (1:1:1, v/v). One week after the seedling emergence, three seedlings per tube were left growing while others were thinned out. Well-watered plants were irrigated on alternate days to keep them at FC during the whole growing period. Water stress was started at the stem elongation stage (Zadoks growth stage of 37) by withholding water until 75% soil available moisture depletion, using soil water depletion curve (equivalent to a water content of 12 v/v % measured by Extech MO750 Soil Moisture Meter, USA). At this point, traits were measured and then soil moisture was brought to FC. Water stressed plants were irrigated in about 5 days intervals.

Measurements

Relative water content (RWC): leaves were detached and weighed immediately to obtain fresh weight (FW), then floated on distilled water for 4 h and weighed to obtain turgor weight (TW), and therafter were dried in the oven at 70 °C for 24 h to obtain the dry weight (DW). RWC was calculated by the formula given by Boyer *et al*. (2008):

$$\mathrm{RWC}(\%) = \frac{\mathrm{Fw} - \mathrm{Dw}}{\mathrm{Tw} - \mathrm{Dw}} \times 100$$

Excised leaf water loss (ELWL): leaves were detached and immediately weighed to obtain FW.

FW. Leaves were then wilted for 4 hours under laboratory condition (20 °C, in the dark), and weighed again (W4h). Then, leaves were dried in the oven and their dry weight (DW) was obtained. ELWL was calculated according to David (2010):

$$\text{ELWL}(\%) = \frac{\text{Fw} - \text{W4h}}{\text{Dw}} \times 100$$

Cell membrane injury (CMI): leaf blades were cut into 1-cm-long sections. 0.5 g leaf samples were placed into vials and were washed with distilled water. 10 ml of distilled water was added to each vial. Vials were heated at 40 °C for 30 min and then were held at 10 °C for 24 h, then warmed to room temperature and thereafter electrical conductivity was measured (C1). The tubes were heated in boiling water for 10 min and cooled and then electrical conductivity was measured (C2). CMI was measured according to Blum and Ebercon (1981):

$$\text{CMI} = \text{C1}/\text{C2}$$

Chlorophyll fluorescence*:* The ratio of variable (Fv) to maximal (Fm) fluorescence in the dark-adapted state, as a measure of potential quantum yield of photosystem II (Fv/Fm), and initial fluorescence (F0) were measured in the flag leaves of three plants per pot using OS30P fluorometer.

Stomatal conductance or gas exchange (Gs): This trait was measured in flag leaves of three plants per pot using Decagon SC-1 leaf porometer.

Stomatal conductance or gas exchange (Gs): This trait was measured in flag leaves of three plants per pot using Decagon SC-1 leaf porometer.

Leaf thickness (LT) and specific leaf area (SLA): These traits were estimated using the formula given by Vile *et al.* (2005):

$$\text{LT} = (\text{SLA} \times \text{LDMC})^{-1}$$

where LDMC (leaf dry matter content) was the ratio of leaf dry mass to saturated fresh mass and SLA was regarded as the ratio of leaf area to leaf dry mass.

Root characteristics: Root dry weight (RDW) and root length (RL) were measured after maturity according to Craine *et al.* (2002).

Grain yield (GY): after maturity, grain weights of three plants in each pot were measured and their mean, regarded as grain yield/pot.

Statistical analyses

The diallel analysis was done based on the method of Hayman (1954). The genetic components and parameters in Table 2 were estimated according to Singh and Singh (1984). Significance of genetic components was verified using t-test. Average degree of dominance, broad sense heritability and narrow sense heritability were estimated according to Mather and Jinks (1971). The assumption of no epistasis was verified by the analysis of variance of Wr-Vr and linear regression of Wr on Vr (H_0: b= 1). Genetic components in Table 2 were estimated by electronic spread sheets in the Excel 2010 program. Furthermore, combining ability analysis was done by the Method II, Model I of Griffing (1956). To assess the relative importance of additive and non-additive gene effects, the Baker's variance ratio (2 MSgca/(2 MSgca + MSsca)) was computed according to Baker (1978). SAS 9.2 software was utilized to perform the combining ability analysis.

Table 2. Genetic components and parameters used in the study.

Genetic components	Formula	Genetic parameters	Formula
Additive genetic variance	$D = Vp - E$	Average degree of dominance	$\sqrt{\left(\frac{H_1}{D}\right)}$
Uncorrected dominance variance	$H_1 = Vp + 4\overline{V}_r - 4\overline{W}_r - \frac{5n-4}{n}E$	Relative distribution of positive and negative genes among parents	H2/4H1
Corrected dominance variance	$H_2 = 4\overline{V}_r - 4V_{\bar{r}} - \frac{4(n-1)}{n}E$	Narrow sense heritability	$Hn = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}$
Covariance of additive and dominance effects	$F = 2Vp - 4\overline{W}_r - \frac{2(n-2)}{n}E$	Broad sense heritability	$Hb = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}$
Environmental variance	$E = \frac{MSE}{r}$	Relationship of the favorable alleles with dominance	rYr (Wr + Vr)

E: Environmental variance; $\overline{V}_r$: mean of the array variances; $\overline{W}_r$: mean of the covariances of arrays with parents; $V_{\bar{r}}$: variance of array means; V_p: variance among parents; n: number of parents.

Results

The results of the goodness of fit for the additive-dominant model are shown in Table 3. Non-significant Wr-Vr mean squares for treatments (crosses) indicate the adequacy of additive-dominant model for all traits except for Gs under non-stress condition. However, the slope of linear regression for F_0 (under stress), Fv/Fm (non-stress) and Gs (non-stress), was significantly lower than unity and additive-dominant model did not fit (Table 3). Genetic parameters of the diallel experiment are shown in Table 4. Additive effect (D component) was significant for all traits, except for GY in both environments and RWC, RDW and LT in the normal environment, indicating the presence of additive effects in the control of most of the traits under study. For most traits, significant additive effects in Hayman's method were corresponded with the significant GCA source of variation in Grifting's method (Table 5). Unweighted and weighted dominance variance components (H_1 and H_2, respectively) were also highly significant for all of the traits except for RDW (non-stress) and LT (non-stress), indicating the importance of dominant genetic effects in governing the traits under investigation. However, SCA mean squares (as a measure of dominance variance) in Grifting's method were significant only for GY, RDW, LT, Gs and RWC under non-stress condition. Differences observed between the two methods, has been mentioned by Singh and Singh (1984). The estimates of F component were generally non-significant except for RL, Gs and Fv/Fm under stress and F_0 and SLA in the normal environment. Positive value for F is an indication of higher frequency of dominant alleles in the parents. The proportion of $H_2/4H_1$ was lower than 0.25 for all traits, indicating the asymmetric distribution of the positive and negative alleles in the parents. This means that some parents are significantly better than others. Average degree of dominance was higher than unity for all traits, indicating the presence of over-dominance in controlling the traits under study. Contribution of over-dominance gene action was corresponded with high heterosis for RWC, SLA and ELWL (Table 4).

The broad sense heritability (Hb) values were high in most cases and ranged from 0.53 for RL to 0.95 for Gs. Among the traits, CMI had the highest narrow sense heritability (0.47), followed by SLA (0.37), ELWL (0.35) and RWC (0.31). The differences observed between the Hn and Hb reflected the presence of the dominant genetic effects on the control of the characters evaluated in this study.

The correlation coefficients between the parental means and order of dominance "rYr (Wr + Vr)" which indicates the relation between the favorability of alleles and dominance, were significantly negative for GY, SLA and CMI (Table 4), indicating that in GY and SLA, dominant alleles are favorable and in CMI, recessive alleles are favorable (higher cell membrane injury is undesirable). Based on GCA effects (Table 6) it was seen that Parent 1 had favorable alleles for RWC, RL, Gs, CMI, F_0 and ELWL, parent 2 had favorable alleles for grain yield, RL, RDW and Gs, parent 3 had favorable alleles for RL, Fv/FM, SLA and LT, parent 4 had favorable alleles for grain yield, RL and SLA under non-stress condition and for RWC under stress condition and parent 5 had favorable alleles for grain yield, Fv/FM, F_0, ELWL and LT, considering that for ELWL, CMI, LT and F_0 lower values are favorable.

Discussion

Based on the results of this experiment it can be ststed that most of the traits adequately can be described by the additive-dominance model. Results showed that additive effects as well as dominant effects were significant in relation to most traits. In general, all had high broad sense heritability, indicating higher genetic variance for the measured traits. Since the average degree of dominance was higher than unity for all traits, the greater importance of dominance effects was confirmed. Similar results were obtained by Rebetzke *et al*. (2003), Shahbazi *et al.* (2013) and Shayan *et al*. (2018) about the genetic control of physiological traits in wheat. Due to the importance of dominance gene action in the control of characters under study, it is suggested that the evaluation of genotypes should be postponed to the advanced generations of inbreeding when the frequency of heterozygote genotypes within families has decreased. Regarding to high values for degree of dominance in one hand and high Baker's ratio (which is an indication of the predominant role of additive gene effects) on the other hand, it seems that the average degree of dominance was overestimated due to the failure of independent distribution of genes in the parents. It may also be possible that Baker's ratio was over estimated, since GCA variance may contain some portion of dominance (Singh and Singh 1984).

Narrow sense heritability of the traits was in general low, especially in GY, RDW and RL, under stress and RWC in non-stress condition. Painawadee *et al*. (2009) also estimated low narrow sense heritability for RDW, RL, root volume and SLA in Peanut. Similarly Shayan *et al*. (2018) estimated the narrow sense heritability of the morpho-physiological traits of wheat as 0.24-0.43 in the normal condition and 0.22-0.38 in the water stress condition, respectively. According to Tuberosa (2012) most of the traits that are related to crop performance under drought conditions usually have low (0.3-0.4) or intermediate (0.4-0.7) heritability which reduces the effectiveness of phenotypic selection. Estimate of narrow sense heritability of RWC was 0.11 and 0.31 under normal and drought stress conditions, respectively. Important role of non-additive gene effects in the genetic control of RWC in wheat was reported by Golparvar *et al*. (2013). In their study narrow sense heritability of RWC under drought stress was estimated as 0.32. In our study, among root characteristics, RDW had relatively higher heritability than RL. Similar results were obtained also in the study of Painawadee *et al*. (2009). Breeding for improved root system in cereals could significantly improve their yield under drought (Craine *et al*. 2002). Narrow sense heritability of SLA was 0.37. According to Rebetzke *et al*. (2004)

Table 3. Goodness of fit of additive-dominant model for evaluated traits.

Character	Environment	Heterogeneity of Wr-Vr		t-test of b on the null-hypothesis	
		MSt	MSe	H_0: b= 0	H_0: b= 1
GY	S	0.014^{ns}	0.074	0.69*± 0.212	0.69^{ns}± 0.212
	NS	0.840^{ns}	0.48	0.76*± 0.234	0.76^{ns}± 0.234
RWC	S	92.4^{ns}	172.9	0.60*± 0.120	0.60^{ns}± 0.120
	NS	3.51^{ns}	2.22	0.60*± 0.195	0.56^{ns}± 0.19
RL	S	487.7^{ns}	2231	0.94*± 0.223	0.94^{ns}± 0.223
	NS	935.7^{ns}	3890	1.12*± 0.348	1.12^{ns}± 0.348
RDW	S	0.001^{ns}	0.003	0.99*± 0.213	0.99^{ns}± 0.213
	NS	0.003^{ns}	0.01	0.67*± 0.154	0.67^{ns}± 0.154
F0	S	65.1^{ns}	54.3	0.14^{ns}± 0.120	0.14*± 0.120
	NS	88.0^{ns}	31.2	0.89*± 0.276	0.89^{ns}± 0.276
Fv/Fm	S	1711^{ns}	1974	0.84*± 0.257	0.84^{ns}± 0.257
	NS	2612^{ns}	5092	0.51^{ns}± 0.307	0.51^{ns}± 0.307
Gs	S	1583^{ns}	562	0.68*± 0.213	0.68^{ns}± 0.213
	NS	239911*	62477	-0.13^{ns}± 0.24	-0.13*± 0.24
CMI	NS	202.9^{ns}	386.2	0.54*± 0.168	0.54^{ns}± 0.168
ELWL	NS	97.9^{ns}	19.7	0.57*± 0.175	0.57^{ns}± 0.175
SLA	NS	12141^{ns}	89932	0.73*± 0.149	0.73^{ns}± 0.149
LT	NS	1.19^{ns}	1.88	0.70*± 0.152	0.70^{ns}± 0.152

Wr: array covariance; Vr: array variance; b: regression coefficient of array covariances with array variances; MSt: mean squares of treatments (crosses); MSe: mean squares within crosses; S: stress; NS: non-stress; ns,* and ** non-significant and significant at 5% and 1% probability levels, respectively; GY: grain yield; RWC: relative water content; RL: root length; RDW: root dry weight; F0: initial fluorescence; Fv/Fm: quantum yield of photosystem II; Gs: gas exchange; CMI: cell membrane injury; ELWL: excised leaf water loss; SLA: specific leaf area; LT: leaf thickness.

SLA had small to moderate narrow-sense heritability. Rapid leaf expansion early in the growing season may increase weed competitiveness, water use efficiency and grain yield in winter cereals. Selection for a larger SLA may contribute to genetic increase in early vigor because this character is partly associated with a larger SLA (Rebetzke *et al*. 2004). In our study narrow sense heritability of ELWL was estimated as 0.35. The results of Chandra and Islam (2003) suggested the involvement of additive genes in the control of ELWL. Based on our results, narrow sense heritability of stomatal conductance was estimated as 0.27. Similarly Jatoi *et al*. estimated the narrow sense heritability of stomatal conductance in wheat as 0.39 under water stress condition (2012). Chlorophyll fluorescence parameters also had low narrow sense heritability which is in accordance with the results of other studies (Shahbazi *et al*. 2009; Čepl *et al*. 2016). Based on the results of this experiment, presence of negative heterosis was confirmed for SLA, ELWL and RWC. As a result, F1 progenies had lower SLA (thicker leaves), lower ELWL (non-stomatal water loss) and lower RWC than their parents. RWC assesses the change in leaf water status. However,

Table 4. Estimates of genetic components and related statistics in the half-diallel mating design.

Parameter	GY		RDW		RL		RWC	
	Non-stress	Stress	Non-stress	Stress	Non-stress	Stress	Non-stress	Stress
D	0.25^{ns}±0.29	0. 35^{ns}±0.2	0. 35^{ns}±0.19	0. 35*±0.13	28.5**±3.8	47.9**±3.3	2.9^{ns}±1.1	24.3**±2.4
H1	2.45*±0.81	1.45*±0.52	1.20^{ns}±0.50	1.70**±0.36	130.3**±10.5	295**±8.9	17.2**±2.8	76.2**±6.5
H2	1.70^{ns}±0.73	1.30*±0.46	0. 97^{ns}±0.46	1.50**±0.32	109.3**±9.5	264**±8.1	16.2**±2.6	74.8**±5.9
F	0. 65^{ns}±0.75	0.11^{ns}±0.47	0. 34^{ns}±0.46	0. 38^{ns}±0.34	7.35^{ns}±9.6	43.9**±8.2	2.8^{ns}±2.6	3.3^{ns} ±5.9
Average degree of dominance	3.15	6.43	1.8	2.2	2.13	2.48	2.45	1.76
H2/4H1	0.17	0.22	0.20	0.23	0.21	0.22	0.23	0.25
H_n	0.27	0.11	0.29	0.12	0.23	0.17	0.11	0.31
H_b	0.89	0.86	0.90	0.93	0.53	0.78	0.84	0.83
rYr (Wr + Vr)	-0.69^{ns}	-0.75*	-0.46^{ns}	-0.47^{ns}	-0.35^{ns}	-0.48^{ns}	-0.27^{ns}	0.08^{ns}
Heterosis+	0.64	0.66	6.4	5.0	1.6	0.57	-32.5	-33.18

Table 4 Continued

Parameter	LT	SLA	ELWL	Gs	Fv/Fm	F0	CMI
	Non-stress	Non-stress	Non-stress	Stress	Stress	Non-stress	Stress
D	0.07^{ns}±0.45	294** ±14.4	10.7*±2.4	61.9**±4.9	47.8**±2.7	15.1**±2.1	34.5**±2.6
H1	0.73^{ns}±1.22	14112** ±39	46.8**±6.6	344.3**±13.2	116.4**±7.3	39.3**±5.8	60.5**±7.1
H2	0.64^{ns}±1.11	3545** ±35.4	41.5**±5.9	297.3**±11.9	94.4**±6.6	32.8**±2.3	50.8**±6.4
F	0.049^{ns}±1.13	-498**±36.1	1.35^{ns}±6.1	50.6**±12.2	47.3**±6.7	15.2*±5.3	10.7^{ns}±6.6
Average degree of dominance	3.2	3.7	2.1	2.35	1.56	1.61	1.32
H2/4H1	0.22	0.22	0.22	0.22	0.20	0.21	0.21
H_n	0.20	0.37	0.35	0.27	0.25	0.21	0.47
H_b	0.84	0.85	0.85	0.95	0.77	0.76	0.83
rYr (Wr + Vr)	-0.05^{ns}	-0.94*	0.57^{ns}	0.47^{ns}	-0.55^{ns}	0.66^{ns}	-0.82*
Heterosis+	-0.76	-130.20	-13.53	-6.80	1.57	-1.83	-0.60

ns,* and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively; +: as % of the mean. GY: grain yield; RDW: root dry weight; RL: root length; RWC: relative water content; LT: leaf thickness; SLA: specific leaf area; ELWL: excised leaf water loss; Gs: gas exchange; Fv/Fm: quantum yield of photosystem II; F0: initial fluorescence; CMI: cell membrane injury; D: additive genetic variance; H1: uncorrected dominance variance; H2: uncorrected dominance variance; F= covariance of additive and dominance effects; H2/4H1: relative distribution of positive and negative genes among parents; H_n: narrow sense heritability; H_b: broad sense heritability; rYr (Wr + Vr): relationship of the favorable alleles with dominance.

the method may not be valid due to osmotic adjustment. This is due to the fact that leaves with a higher concentration of solutes will take up more water and may lead to anomalously low estimates of relative water content (Boyer *et al*. 2008). Results also showed that for traits under study, significant relationship was found between dominance and favorability of alleles only in GY (under stress), SLA and CMI. This means that a parent with more dominant alleles for GY or SLA will be more favorable. Due to difficulty of measuring stomatal conductance and root features in field, this experiment was carried out as an alternative to root and stomatal conductance phenotyping in field. The major disadvantage of these researches is that the environment is not natural, suggesting great caution in extrapolating the results to field-grown plants. In spite of the importance of physiological traits as selection criteria in breeding programs, presence of large dominance effects should not be neglected and selection for these traits should be delayed until after some homozygosity was achieved. However, the dominance effects can be exploited in the breeding of F_1 hybrids in wheat after overcoming the barriers of producing hybrid varieties in this crop plant.

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Table 5. General combining ability (GCA) and specific combining ability (SCA) mean squares for evaluated traits from a 5 × 5 half-diallel cross in wheat.

Parameter	df	GY		RDW		RL		RWC	
		Non-stress	Stress	Non-stress	Stress	Non-stress	Stress	Non-stress	Stress
GCA	4	0.177^{ns}	0.055^{ns}	0.031**	0.022**	75.69*	50.11^{ns}	0.81^{ns}	24.94*
SCA	10	0.626**	0.334**	0.025**	0.038**	29.98^{ns}	40.99^{ns}	2.76**	12.11^{ns}
Error	28	0.082	0.0476	0.0037	0.003	19.50	23.45	0.87	6.16
Baker's ratio		36.1%	24.7%	71.3%	53.1%	83.5%	70.9%	37%	80.5%

Table 5 Continued

Parameter	df	LT	SLA	ELWL	Gs	Fv/Fm	F0	CMI
		Non-stress	Non-stress	Non-stress	Stress	Stress	Non-stress	Stress
GCA	4	0.0111*	1083*	15.98**	55.79**	36.67 *	6.50^{ns}	44.07**
SCA	10	0.0094*	564.5^{ns}	5.82^{ns}	54.87**	16.73^{ns}	7.61^{ns}	10.52^{ns}
Error	28	0.004	272.7	3.025	5.5	10.3	3.52	6.14
Baker's ratio		70.3%	79.3%	84.6%	67.0%	81.4%	63.0%	89.3%

ns,* and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively; GY: grain yield; RDW: root dry weight; RL: root length; RWC: relative water content; LT: leaf thickness; SLA: specific leaf area; ELWL: excised leaf water loss; Gs: gas exchange; Fv/Fm: quantum yield of photosystem II; F0: initial fluorescence; CMI: cell membrane injury.

Table 6. General combining ability (GCA) of parents in a 5 × 5 half- diallel cross for evaluated traits of wheat.

Character	Environment	Parent					SE of gcai	SE of gcai-gcaj
		1	2	3	4	5		
GY	S	-0.03	0.06	-0.02	-0.12	0.11	0.005	0.014
	NS	-0.04	0.19	-0.24	0.06	0.04	0.009	0.023
RWC	S	1.37	-1.44	-2.08	3.39	-1.25	1.06	2.64
	NS	0.20	-0.36	-0.19	-0.30	0.64	0.15	0.37
RL	S	1.57	1.67	1.67	-4.52	-0.38	2.68	6.70
	NS	-5.51	2.50	2.50	0.68	-0.17	2.23	5.57
RDW	S	0.013	0.023	-0.025	-0.080	-0.068	0.0003	0.0008
	NS	0.106	0.010	-0.025	-0.016	-0.075	0.0004	0.0011
F0	NS	-1.21	0.09	0.38	1.33	-0.58	0.40	1.01
Fv/Fm	S	-0.24	-1.29	2.19	-3.00	2.33	1.17	2.95
Gs	S	4.33	2.81	-3.18	-0.73	-3.24	0.94	2.35
CMI	NS	-3.56	0.06	-1.48	2.12	2.36	0.70	1.75
ELWL	NS	-2.19	-0.06	2.92	-0.05	-0.62	0.52	1.29
SLA	NS	-14.24	-1.36	22.24	6.85	-13.49	46.75	116.90
LT	NS	0.020	0.011	-0.082	0.004	0.048	0.0007	0.0017

SE: standard error; S: stress; NS: non-Stress; GY: grain yield; RWC: relative water content; RL: root length; RDW: root dry weight; F0: initial fluorescence; Fv/Fm: quantum yield of photosystem II; Gs: gas exchange; CMI: cell membrane injury; ELWL: excised leaf water loss; SLA: specific leaf area; LT: leaf thickness.

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ژنتیک و وراثت پذیری برخی از صفات فیزیولوزیک در جو تحت تنش خشکی

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چکیده

به منظور تعیین وراثت‌پذیری برخی از صفات فیزیولوژیک درگیاه جو، بذرهای F1 حاصل از یک تلاقی دی الل ۵×۵ به همراه والدین درگلخانه در شرایط بدون تنش و تنش خشکی انتهایی، در ایستگاه تحقیقات کشاورزی دانشگاه آزاد اسلامی واحد اردبیل در سال ۱۳۹۵ کشت گردیدند. صفات فیزیولوژیک و زراعی محتوی نسبی آب برگ، اتلاف آب از برگ جداشده، هدایت روزنه‌ای، صدمه وارده به غشا، پارامترهای فلورسانس کلروفیل، سطح ویژه برگ، ضخامت برگ، طول ریشه، وزن خشک ریشه و عملکرد دانه اندازه گیری شدند. نتایج نشان داد که وراثت پذیری عمومی تمام صفات بالا بود. در بین صفات اندازه گیری شده، صدمه وارده به غشای سیتوپلاسمی دارای بیشترین وراثت پذیری خصوصی بود (۰/۴۷) و سطح ویژه برگ، اتلاف آب از برگ جداشده و محتوی نسبی آب برگ بترتیب با مقادیر ۰/۳۶۹، ۰/۳۵۳ و ۰/۳۱۱ در رتبه‌های بعدی قرار گرفتند. درجه غالبیت متوسط در مورد تمام صفات اندازه‌گیری شده بزرگتر از ۱ بود که حاکی از کنترل کلیه صفت توسط اثر فوق غالبیت ژنی بود. نتایج نشان داد که در عملکرد و سطح ویژه برگ الل‌های غالب و در صدمه وارده به غشای سیتوپلاسمی الل‌های مغلوب، مطلوب می‌باشند. نتایج همچنین نشان داد که نتاج F1 در مقایسه با والدین دارای سطح ویژه برگ، اتلاف آب از برگ جدا شده، محتوی نسبی آب برگ و هدایت روزنه‌ای کمتر و وزن خشک ریشه بیشتری هستند. با توجه به اهمیت بیشتر ارزش‌های غالبیت در کنترل صفات اندازه‌گیری شده، پیشنهاد می‌شود که ارزیابی صفات در نسل‌های تفرق پیشرفته و بعد از رسیدن نتاج به خلوص نسبی انجام گیرد.

واژه‌های کلیدی: تنش خشکی؛ صفات ریشه؛ صفات فیزیولوژیک؛ هدایت روزنه‌ای؛ وراثت پذیری