

GENETIC ANALYSIS OF STOMATAL FEATURES OF SOME BREAD WHEAT CULTIVARS UNDER DIFFERENT WATER REGIMES

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ABSTRACT

Eight diverse wheat genotypes were selected and crossed in all possible combinations to study the inheritance pattern of stomatal related characters under three different irrigation regimes. Knowledge of the stomata responses to different plant water status is necessary for the breeding varieties with more water use efficiency and drought tolerance. Eight bread wheat genotypes as parents and their 28 F1 hybrids were grown using a completely randomized design (CRD) with four replicates at the greenhouse under different water regimes. The stomatal parameters were assessed on both abaxial (lower) and adaxial (upper) leaf surfaces using a light microscope. The stomatal indices i.e. the operating stomatal conductance to water vapor (g_s), the stomatal shape coefficient (SSC) and the potential conductance index (PCI) were estimated using obtained stomatal morphological data. All data were analyzed by both the Griffing and the Hayman diallel methods. Estimates of the genetic components of variation and other genetic parameters indicated that both additive and dominance effects were involved in genetic control of stomatal density and operating stomatal conductance (g_s) under different irrigation regime. The results revealed the sensitivity of both kinds of gene effects to the environmental variations. Moderately high estimates of heritability were recorded. Due to summary of all morpho-anatomical traits, the Sivand and the Parsi varieties and the Marvdasht×Sivand and the Parsi×Pishtase crosses at normal irrigation regime, the Parsi and Pishtase varieties and the Marvdasht×Sivand and the Parsi×Pishtase crosses at stress site and the Sirvan variety and the Sivand×Sirvan and Marvdasht×Sirvan crosses at water holding site are the best varieties and crosses for improvement of stomata related characters among other varieties and crosses. Advanced-generation breeding methods were suggested for improvements of stomata related characters under different water regimes.

Keywords: Combining ability, Diallel analysis, Gas exchange, potential conductance index.

INTRODUCTION

Sustainable food production to meet the future demands in the scenario of global climate change and increasing population is the major challenge to the scientists and policy makers (Pask and Reynolds, 2013). Wheat is the most commonly grown cultivated crop in the world (Akbarabadi *et al.*, 2015; Ahmadi *et al.*, 2012; Ghobadi *et al.*, 2012). However, its production is not reached in accordance with the world population growth and climate changes (Zebarjadi *et al.*, 2012; Geravandi *et al.*, 2011). Wheat yield models indicated that climate change will reduce wheat yield potential in its major producing areas (Valizadeh *et al.*, 2014). Hence, there is strong recommendation to increase the rate of wheat genetic progress for yield, drought tolerance and water use efficiency (Pask and Reynolds, 2013; FAO, 2013). However, the serious problem of wheat production is drought and water deficit in the end of its growth season in the arid and semi-arid areas (Kilic and Yagbasanlar, 2010; Farooq *et al.*, 2009; Talebi *et al.*, 2009). It is estimated that about 65 million hectares of the global wheat production area are affected by drought (FAO, 2013). Therefore, breeding wheat genotypes with relevant drought tolerance features is a key to enhance

productivity and food security in the arid and semi-arid areas.

The major part of water uptake in plants is lost through stomata transpiration (Pei *et al.*, 1998; Saradadevi *et al.*, 2017). Stomata have a strong influence on characteristics associated with photosynthesis and transpiration. Stomata vary in size and density among cultivated varieties within species. Moreover, stomatal characteristics are greatly influenced by environmental conditions. Plants increase their water use efficiency (WUE) by reducing stomatal aperture and thereby transpiration rate under conditions of short-term water stress. In other hand, under prolonged water deficit condition, plants decrease stomatal conductance (g_s) by change in stomatal size and/or stomatal density (SD) (Doheny-Adams *et al.*, 2012; Franks *et al.*, 2012). Stomatal conductance is potentially one of the most significant physiological characters to improve adaptation to drought for selecting a particular pattern of stomatal behavior (Blum *et al.*, 1981; Henzell *et al.*, 1975). Increasing stomatal density improves maximum potential conductance (Franks *et al.*, 2009). On the other hand, Hetherington and Woodward (2003) stated that increasing aperture and/or size dimensions of the stomata will reduce stomatal conductance. Wang and

Clarke(1993) reported that total stomatal pore area positively correlate with stomatal density in wheat genotypes. Also, it has been reported that smaller stomata are able to rapidly adjust their turgor pressure to control water loss and CO₂ influx more efficiently (Franks *et al.*, 2009; Hetherington and Woodward, 2003).

Diallel cross is one of the most complex designs that have been used extensively for the genetic analysis of quantitative characters to obtain information about genetic properties of parental lines or estimates of general (GCA) and specific (SCA) combining abilities and heritability (Iqbalet *et al.*, 2007). Information on general and specific combining ability effects is significant in a breeding program. Diallel cross method provide early information on the genetic behavior of these attributes in the first generation (Topal *et al.*, 2004). To date, several methods have been proposed for the genetic analysis of data from a diallel cross (Griffing, 1956; Hayman, 1954a and b; Jones, 1965). Among various diallel forms, the half diallel methods have certain advantages, giving maximum information about the genetic architecture of a trait, parents and allelic frequency (El-Maghraby *et al.*, 2005; Farshadfar *et al.*, 2011.). Hayman developed the best-known methods for diallelic analysis, exclusively for homozygous parents (Hayman, 1954a and b). Griffing used the half diallel analysis for combining ability (Griffing, 1956). Jones (1965) extended the analysis of variance of a full diallel table to a half diallel table. The main reasons that justify the universal uses of the Griffing's method are its generality, since the parents can be pure lines, clones, populations of a self-pollinated, inbred lines, cross-pollinated or intermediate species, the ease of analysis and interpretation (Griffing, 1956) on the other hand, the Hayman's method, may include statistical and graphical analyses of array variances and covariances and the estimation of several genetic parameters (Farshadfar *et al.*, 2012). As the genetics of drought-related characters is complex and not adequately understood and since little information is available on the genetics of characters associated with drought, it is necessary to assess the estimates of gene effects under variable environmental stress conditions to ensure better prediction and gain under selection (Arraudeau, 1989). This study was aimed to investigating (I) some stomatal features at different irrigation regimes, (II) Evaluation of the relative importance of GCA and SCA in a set of wheat cultivars and their F1 diallel crosses and (III) Evaluation of the genetic properties of some stomatal characters at different moisture environments.

MATERIALS AND METHODS

Plant material and growth condition: Eight bread wheat genotypes as parents and their 28 F1 hybrids listed in Table 1 were grown in a completely randomized design (CRD) with four replicates at different water regimes

(Normal irrigation site (Nor.): 85% of FC i.e. -0.3 bars due to water retention curve, water holding site (W.H.): water used similar to the normal site but water on-hold at flowering stage and water stress site (Str.): 50% of FC i.e. -6.5 bars due to water retention curve, applied at tillering stage) at the greenhouse of the Campus of Agriculture and Natural Resources, Razi University, Kermanshah, Iran in 2015. Germinated seeds of each parent and their 28 F₁ hybrids after 50 days of vernalization at zero degree °C were planted in 432 pots (144 pots per water regime site) measuring 25 cm wide by 30 cm deep, containing two parts (by volume) top soil, one part vermiculite and one part sand. The pots were checked by soil moisture meter digital Lutron model PMS-714 and irrigated weekly with equal amounts of water equivalent to the water regimes that set before for each site. All pots were maintained at 16 h day/ 8 h night and temperature regimes of 30/17°C. Photosynthetic photon flux density at plant height was approximately 20000 μmol m⁻² s⁻¹ during the photoperiod.

Table 1. Cultivar name and pedigree of parents.

P1. Marvdasht (Stm/3/Kal/V543/Jit714)
P2. Bahar (ICW84-0008-013AP-300L-3AP-300L-0AP)
P3. Sivand (Kaus's"/Azadi)
P4. Parsi (Dove"S"/Buc"S"/Darab)
P5. Pishtase (1-27-6275/cf1770//Aldan/Ias58)
P6. Zare (130L1.11//F35.70/Mo73/4/Ymh/Tob//Mcd/3/Lira)
P7. Sirvan (Prl/2*Pastor)
P8. Pishgam (Zhong 87-90/Barekat)

Stomatal density, index and operating stomatal conductance measurements: Stomatal features were assessed on both abaxial (lower) and adaxial (upper) leaf surfaces. 2–3 cm of both the abaxial and adaxial surfaces of the middle flag leaf were coated with clear nail polish and dried. The imprint was then peeled off, mounted on a glass microscope slide, and examined under a light microscope (BX51, Olympus, Japan) as described by Wang and Clarke (1993). Stomatal density (SD) was counted at 400X magnification. Stomatal morphological parameters were measured at 1000X magnification using the same light microscope. Stomatal morphological parameters were: guard cell length (L_s, μm), guard cell pair width (W_s, μm), aperture length (L_a, μm) and aperture width (W_a, μm). For each epidermal peel, 10 stomata were sampled for size and five fields were sampled for density.

The operating stomatal conductance to water vapour (g_s, mol m⁻² s⁻¹) was estimated using a modified version of the Brown and Escombe (1900) equation:

$$g_s = \frac{d_c \times S \times a}{v \times (l + (\pi/2) \sqrt{a/\pi})}$$

where d_c is the diffusivity of H₂O in air (2.43 × 10⁻³ m² s⁻¹), SD is the stomatal density (m⁻²), a is

the mean stomatal pore area (m^2), v is the molar volume of air ($0.024 \text{ m}^3 \text{ mol}^{-1}$), l is the depth of the stomatal pore (m, approximated as the width of a single guard cell) and π is the mathematical constant. The mean stomatal pore area was estimated from:

$$a = \frac{\pi \times W_a \times L_a}{4}$$

where W_a is aperture width and L_a is aperture length. The following obtained indices were estimated:

Stomatal shape coefficient (SSC; Balasooriya *et al.*, 2009):

$$S = 100W_s/L_s$$

Potential conductance index (PCI; Holland and Richardson, 2009):

$$P = W_a L_a S \times 10^{-4}$$

Statistical analysis: All data were subjected to analyses of variance. Data obtained from the 28 F1 progenies and the eight parents were subjected to Griffing's method 2 using a fixed effect model and then analyzed for combining abilities (Griffing, 1956). Genetic components were also shown in Jones (1965) modification of Hayman's approach. The analyses were performed using the Diall98 software (Ukai, 2006) and SAS software (SAS Institute, 2003). The combining ability ratio was calculated according to Baker (1978) as follows:

$$B a \quad r_i = \frac{2M_G}{2M_G + M_S}$$

RESULTS AND DISCUSSION

Analysis of variance: An initial analysis revealed that significant differences existed between all parents and their progenies (F1s) for all morpho-anatomical traits at all sites. Water stress had a significant effect on SSC, PCI and estimation of operating stomatal conductance (g_s). Significant differences were observed due to genotypes for stomatal density, SSC and PCI and estimation of operating stomatal conductance (g_s). The genotypes and irrigations regimes interaction was significant for all the measured traits (Table 2 and 3). Holland and Richardson (2009) showed that stomatal density and guard cell length are both sensitive to environmental conditions and that considerable genotypic variation and phenotypic plasticity occurred in these traits. This is in agreement with the results presented by other authors, who found that stomatal density appears to be relatively plastic compared to stomatal length (Richardson *et al.*, 2001; Fanourakis *et al.* 2014) and therefore, potentially adaptive to environmental change (Lake *et al.*, 2001). Presence of non-significant differences among irrigation levels and significant interaction effect of irrigation and genotypes for stomatal density, suggests that effect of abiotic factors on stomatal size may depend on the genotypes. The study also showed that stomatal shape

and potential and operating gas exchange are sensitive to drought stress, which is consistent with the results obtained in some earlier studies (Baloch *et al.*, 2013; Alam *et al.*, 2011; Ashfaq *et al.*, 2016; Erdal *et al.*, 2016). The mean performance of all irrigation regimes for the stomatal density, SSC index and PCI and g_s of the eight parental lines and 28 F1 crosses are presented in Table 4. Results indicated that the crosses 4×5 with 44.8 stomata per mm^2 at the abaxial surface and 56.16 stomata per mm^2 at the adaxial surface, 3×8 with 46.4 stomata per mm^2 at the abaxial and 51.8 stomata per mm^2 of the adaxial surface and 4×5 with 45.6 stomata per mm^2 at the abaxial and 53.44 stomata per mm^2 at the adaxial surface showed maximum number of stomata per mm^2 at normal, stress and water holding sites, respectively. The SSC index ranged from 14.8 to 36.3 at the abaxial surface and 14.5 to 37.7 at the adaxial surface across all water regimes. Among the crosses, 4×5, 2×4 and 4×5 had highest SSC index at normal, stress and water holding sites, respectively (Table 4). Also, Maximum PCI at both surfaces was recorded by crosses number 1×3 and 1×4 at normal and water holding sites, respectively, and the P1 (1×1) at water stress site. The g_s for genotypes ranged from 0.45 to 2.49 $\text{mol m}^{-2} \text{s}^{-1}$ at the abaxial surface and 0.69 to 3.2 $\text{mol m}^{-2} \text{s}^{-1}$ across all water regimes. The crosses 1×3, 2×8 and 1×4 showed highest g_s for normal, stress and water holding sites, respectively. The results corroborate with finding of Alam *et al.* (2011) who reported higher stomatal density on the adaxial surface compared with the abaxial surface. In the presence of abiotic stress, the stomata density was increased, but the stomata size decreased to reduce stomatal conductance (Fanourakis *et al.* 2014). Sufficient genetic variability is present for the mentioned morpho-anatomical traits and indices which has been a pre-requisite for launching any breeding program and for further genetic studies (Singh and Chaudhary, 1999).

Analysis of combining abilities: The mean squares of combining abilities revealed that the variance due to GCA (σ_{gca}^2) and the variance SCA (σ_{sca}^2) were significant for all characters at all sites (Table 5). Therefore, both additive and non-additive gene effects were involved in genetic control of all characters examined. The similar result was reported in other works (Ashfaq *et al.*, 2016; Walton, 1974).

Combining abilities is helpful in identifying best sources among the genotypes used. The estimates of GCA effects of the various parents for the stomatal density, SSC, PCI and g_s (Table 6) revealed that due to summary of all morpho-anatomical traits, the parent number 3 and 4 at normal site, parent number 4 and 5 at stress site and parent number 7 at water holding site show highest positive GCA values and are the best general combiners for improvement of stomata related characters at both surfaces. Among 28 cross combinations (Table 7),

Table 2. Combined analysis of variance for the characters under investigation.

S.O.V	df	Stomatal density		SSC		PCI		g _s	
		Abaxial surface	Adaxial surface	Abaxial surface	Adaxial surface	Abaxial surface	Adaxial surface	Abaxial surface	Adaxial surface
Irrigation	2	57.5ns	93.8ns	347**	1431**	0.702**	1.278**	24.83**	39.65**
E1	9	17.9	86.13	19.95	18.02	0.001	0.001	0.08	0.241
genotypes	35	329**	337**	98.45**	64.01**	0.01**	0.01**	0.468**	0.498**
Irri.*gen	70	81.3**	122.2**	30.35**	29.70**	0.004**	0.006**	0.202**	0.339**
error	315	16.1	32.2	16.19	14.51	0.001	0.002	0.0497	0.0847
CV (%)		11.99	13.94	17.17	16.58	21.95	20.19	17.69	18.15

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

SSC: stomatal shape coefficient, PCI: Potential conductance index, g_s: operating stomatal conductance to water vapor

Table 3. Analysis of variance for the characters under investigation.

S.O.V	df	Stomatal density						SSC					
		Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
		Nor.	Str.	W.H.	NOR.	Str.	W.H.	Nor.	Str.	W.H.	NOR.	Str.	W.H.
Genotypes	35	170.32**	146.1**	183.37**	182.6**	224.2**	174.26**	46.42**	57.65**	55.08**	57.10**	28.53**	37.79**
Error	108	16.08	17.45	14.85	33.10	37.43	30.59	22.41	10.27	16.21	24.64	9.97	9.22
CV (%)		11.99	12.35	11.58	13.56	15.16	13.16	19.06	14.89	16.72	19.1	16.17	12.71

S.O.V	df	PCI						g _s					
		Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
		Nor.	Str.	W.H.	NOR.	Str.	W.H.	Nor.	Str.	W.H.	NOR.	Str.	W.H.
Genotypes	35	0.011**	0.003**	0.005**	0.013**	0.004**	0.003**	0.47**	0.18**	0.23**	0.65**	0.32**	0.21**
Error	108	0.002	0.001	0.001	0.003	0.001	0.001	0.093	0.039	0.02	0.154	0.06	0.05
CV (%)		18.22	24.04	25.47	17.1	20.28	20.52	17.11	19.15	14.53	17.16	19.43	16.7

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

Nor.: Normal Irrigations with 85% FC, Str.: Stress Site with 50 % FC, W.H.: water holding at flowering stage.

SSC: stomatal shape coefficient, PCI: Potential conductance index, g_s: operating stomatal conductance to water vapor

Table 4. Mean comparison of the characters under investigation.

Cross	Stomatal density (per mm ²)						Stomatal shape coefficient (SSC)					
	Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
1×1	28.96	29.28	28.64	39.68	32	41.12	23.57	19.01	22.65	24.01	20.28	22.09
1×2	27.68	27.52	28.96	37.12	39.04	38.08	23.47	18.67	24.57	26.82	18.94	24.6
1×3	39.04	35.36	39.04	48.16	40.32	47.2	20.93	19.77	20.86	21.49	18.75	21.31
1×4	40.32	37.28	41.44	42.88	37.76	41.92	26.96	19.29	27.47	27.45	19.65	25.57
1×5	26.88	35.36	25.6	32.96	42.72	32	24.58	25.01	21.14	27.34	23.1	19.75
1×6	28.96	29.28	29.12	43.36	37.28	41.28	26	19.99	24.18	27.4	19.63	21.84
1×7	33.28	33.6	31.68	47.84	50.56	48.16	20.42	20.66	20.88	23.25	18.87	21.02
1×8	28.48	29.28	27.52	26.56	39.04	25.6	25.35	22.93	23.07	26.02	19.51	21.69
2×2	25.6	20.8	24.64	32.96	25.6	36.8	30.4	16.64	27.08	26.99	18.96	25.34
2×3	35.68	34.08	34.4	42.08	38.4	42.4	23.35	14.76	22.36	30.53	14.85	22.67
2×4	41.44	36	40.8	45.76	39.68	44.48	26.65	33.35	25.04	29.77	22.45	23.63
2×5	31.2	42.08	34.88	42.88	45.12	41.76	26.16	22.58	24.06	28.29	19.81	21.78
2×6	40.48	38.4	41.12	40.32	42.08	37.28	26.11	19.73	23.12	27.49	22.61	24.09
2×7	28.64	25.6	28.96	44	32.32	40	23.78	23.58	21.87	25.92	21.95	21.72
2×8	44.32	37.12	43.52	43.2	52.48	41.76	30.06	17.33	33.6	31.68	15.15	29.99
3×3	27.68	37.92	28	36.96	57.92	36	22.95	28.49	24.11	23.48	24.5	24.65
3×4	40.8	40.32	40	48.48	50.56	45.12	23.83	21.8	23.84	22.32	18.21	24.23
3×5	28	30.56	27.36	43.36	39.04	42.08	24.25	19.9	22.51	25.43	21.34	23.11
3×6	34.88	32.96	34.72	49.92	32.96	46.56	24.32	25.11	23.3	26.21	20.31	20.96
3×7	30.56	31.2	29.92	33.92	38.4	33.28	29.01	24.11	30.11	32.88	21.77	32.01
3×8	36.64	46.4	35.36	48.16	51.84	48.16	21.49	21.53	24.57	37.73	22.72	23.54
4×4	33.76	48.16	32.16	35.04	36.64	32.32	24.26	24.1	22.75	23.78	19.44	23.12
4×5	44.8	37.28	45.6	56.16	47.52	53.44	35.81	30.06	36.34	31.3	18.82	30.96
4×6	43.84	35.36	44.48	45.12	37.92	41.12	23.11	23.58	21.85	23.47	20.81	21.44
4×7	30.56	36	29.28	43.04	33.6	41.44	24.44	26.51	22.23	24.6	21.61	19.8
4×8	33.92	30.56	32.64	40.32	41.44	38.08	20.89	23.04	20.11	21.29	18.77	19.08
5×5	32	28.64	32.32	47.04	31.68	44.8	23.74	21.18	24.11	24.54	18.29	24.47
5×6	29.6	32.96	29.6	46.4	40.8	48.48	27.72	17.94	26.11	28.08	15.48	23.76
5×7	29.92	31.04	29.28	41.44	36.64	39.68	22.78	19.42	21.19	24.8	14.54	20.48
5×8	38.4	24.48	37.28	51.84	29.92	50.88	22.38	20.46	21.49	24.12	15.83	23.9
6×6	20.16	39.04	18.88	30.24	45.76	28.64	20.21	20	19.76	20.73	15.62	20.4
6×7	46.72	31.68	47.2	43.04	42.72	42.4	28.33	21.99	26.56	27.82	25.1	22.79
6×8	23.84	30.56	23.84	32.32	22.56	32	20.43	16.98	19.93	21.26	18.95	19.54
7×7	27.84	34.72	26.88	31.2	45.76	29.12	23.44	21.51	23.89	23.93	21.21	24.22
7×8	34.72	35.36	33.92	47.52	40.16	45.76	27.51	20.27	28.22	25.29	23.01	25.84
8×8	28.16	44.48	27.2	34.4	42.08	31.68	18.54	19.29	18.2	19.13	19.09	18.25
mean	33.3	34.2	33.0	41.5	40.0	40	24.6	21.7	24.0	26.0	19.7	23.2
LSD (1%)	7.4	7.7	7.1	10.7	11.3	10.3	8.8	5.9	7.5	9.2	5.9	5.6

cross	Potential conductance index (PCI)						Operating stomatal conductance (gs; mol H ₂ O m ⁻² s ⁻¹)					
	Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
1×1	0.2016	0.0752	0.1168	0.2656	0.096	0.1712	1.44	0.80	0.92	1.91	1.04	1.39
1×2	0.1936	0.12	0.1008	0.2656	0.1136	0.16	1.52	1.02	0.90	2.01	1.09	1.38
1×3	0.3152	0.0832	0.1568	0.4176	0.1312	0.2032	2.49	0.96	1.24	3.20	1.39	1.58
1×4	0.304	0.128	0.2208	0.3424	0.1472	0.2048	2.14	1.37	1.60	2.36	1.37	1.56
1×5	0.1824	0.1056	0.1056	0.2592	0.096	0.1456	1.49	1.11	0.93	2.29	1.00	1.31
1×6	0.192	0.12	0.0944	0.288	0.1472	0.1504	1.51	1.02	0.83	2.18	1.31	1.37
1×7	0.264	0.1056	0.096	0.408	0.1904	0.1696	1.89	0.93	0.92	2.89	1.97	1.57
1×8	0.1632	0.0848	0.1008	0.1536	0.136	0.0976	1.39	0.81	0.91	1.16	1.44	0.89
2×2	0.1472	0.0752	0.104	0.2224	0.1152	0.1552	1.03	0.75	0.81	1.58	1.04	1.27
2×3	0.3216	0.1552	0.112	0.28	0.1216	0.1536	2.14	1.46	0.96	1.97	1.48	1.31
2×4	0.2624	0.0848	0.1424	0.3104	0.112	0.1504	1.96	0.73	1.22	2.24	1.17	1.39
2×5	0.2128	0.168	0.1408	0.2736	0.1456	0.1728	1.54	1.41	1.15	1.99	1.42	1.48
2×6	0.312	0.088	0.1648	0.304	0.12	0.1552	2.26	0.97	1.33	2.23	1.18	1.29
2×7	0.192	0.08	0.0928	0.28	0.096	0.1392	1.50	0.67	0.81	2.18	1.01	1.23
2×8	0.2992	0.1264	0.1744	0.3104	0.1904	0.1824	2.01	1.23	1.29	2.07	1.97	1.45
3×3	0.1584	0.1296	0.0768	0.2272	0.1888	0.112	1.30	1.18	0.75	1.81	1.72	1.05
3×4	0.2304	0.12	0.1296	0.2912	0.1424	0.1456	1.88	1.15	1.21	2.39	1.50	1.41
3×5	0.2384	0.1072	0.104	0.368	0.1472	0.1728	1.69	1.06	0.88	2.54	1.33	1.43
3×6	0.256	0.0848	0.1152	0.3744	0.0752	0.1776	1.70	0.79	1.00	2.54	0.88	1.53
3×7	0.2096	0.1056	0.12	0.24	0.1296	0.1408	1.52	0.97	0.90	1.68	1.18	1.05
3×8	0.2368	0.1232	0.1456	0.3008	0.1504	0.1744	1.91	1.29	1.11	1.99	1.47	1.54
4×4	0.2128	0.1328	0.1088	0.2336	0.1344	0.112	1.65	1.34	0.93	1.78	1.39	0.99

4×5	0.2736	0.16	0.1552	0.3552	0.1216	0.1824	1.88	1.15	1.09	2.48	1.35	1.43
4×6	0.2848	0.0624	0.1264	0.3184	0.0704	0.1312	2.43	0.86	1.25	2.57	0.99	1.24
4×7	0.2496	0.0912	0.1056	0.344	0.16	0.1552	1.79	0.98	0.87	2.51	1.30	1.39
4×8	0.2112	0.104	0.1152	0.312	0.1168	0.1536	1.70	1.00	1.05	2.31	1.26	1.36
5×5	0.1808	0.1056	0.0928	0.2976	0.0992	0.1472	1.77	0.86	1.04	2.79	1.04	1.58
5×6	0.1776	0.1488	0.0976	0.2864	0.112	0.1696	1.43	1.20	0.87	2.23	1.14	1.63
5×7	0.1952	0.08	0.1008	0.2816	0.1088	0.1552	1.58	0.92	0.97	2.26	1.26	1.49
5×8	0.2864	0.08	0.1344	0.4064	0.0928	0.1872	1.96	0.78	1.09	2.71	1.02	1.50
6×6	0.1232	0.112	0.0512	0.2048	0.176	0.0896	0.96	1.18	0.45	1.55	1.71	0.75
6×7	0.3248	0.0912	0.1872	0.3376	0.1392	0.152	2.26	0.90	1.63	2.21	1.35	1.38
6×8	0.2496	0.0752	0.088	0.288	0.0576	0.1216	1.82	0.92	0.83	2.21	0.69	1.16
7×7	0.2496	0.1072	0.088	0.2992	0.1328	0.1056	1.68	1.10	0.71	1.97	1.34	0.83
7×8	0.248	0.1056	0.1408	0.3568	0.0976	0.1968	1.74	1.04	1.09	2.56	0.88	1.62
8×8	0.248	0.1248	0.0832	0.3072	0.088	0.12	1.70	1.40	0.73	2.16	1.18	1.02
mean	0.234	0.107	0.119	0.300	0.125	0.153	1.74	1.04	1.01	2.21	1.27	1.33
LSD (1%)	0.083	0.059	0.059	0.102	0.059	0.059	0.565	0.366	0.262	0.728	0.454	0.415

the crosses 1×3 and 4×5 at normal site and the crosses 1×3 and 4×5 at stress site and the crosses 3×7 and 1×8 at water holding site were identified as good specific combiners due to a summary of stomata related characters at both surfaces.

Components of genetic variance and genetic parameters: Estimation of variance components and genetic parameters are presented in Table 8 and 9. Jones' ANOVA (Table 8) revealed that both additive (a) and dominance (b) components is significant for the stomatal density at both surfaces and g_s at the adaxial surface across all irrigation regimes. The SSC index of both leaf surfaces showed significant additive (a) and dominance (b) effects at normal and stress sites but at water holding site, additive (a) effect was significant only at the adaxial surface. The PCI of both leaf surfaces showed significant dominance (b) effect across all irrigation regimes but at the stress and water holding sites, additive (a) effect was significant only at the adaxial surface. Also, the g_s at the abaxial surface showed significant additive (a) and dominance (b) effects at stress and water holding sites but only dominance (b) effect was significant at normal site.

Mean square of dominance (b1) and dominance due to arrays (b2) were significant for the stomatal density of both surfaces at normal and water holding sites, PCI of the abaxial surface at the normal and water holding sites, g_s at normal and water holding sites. Significant b1 component showed that F1 progenies had higher mean than all parent averages but significant b2 indicated that the number of dominant alleles varies between the eight parents. Mean square of residual dominance effects (b3) was significant for all stomatal related characters and showed that the dominance effects are specific to particular crosses (Table 8).

The additive component of variance (D) was found to be the significant for stomatal density of both surfaces at stress and water holding sites but at normal site, the additive component was significant only at the abaxial surface (Table 9). Also for g_s , the additive component of variance (D) was found to be significant at both surfaces at stress and water holding sites but at

normal site, the additive component was significant only at the adaxial surface. The additive component of variance (D) was found to be significant for PCI of the adaxial surface only at stress site. This indicated that additive component was important in the inheritance of these characters under such conditions. Non-significant values of additive variance were observed for the remaining cases (Table 9). Values of dominant component of variance (H_1 and H_2) were significant for all characters under investigation. Obviously, the magnitudes of both types of dominant variance (H_1 and H_2) were much higher than the additive component (D) indicating the importance of the dominant than the additive component of variance in the inheritance of these traits. Comparable results reported by Lamari and Fayt (2015) and Khan *et al.*, (2011) in wheat.

The F component was significant for stomatal density and g_s of both surfaces and PCI of the adaxial surface at stress site that indicated the presence of unequal frequency of dominant and recessive genes for these characters. In other hand, for remaining cases, the non-significant F component indicated equal frequency of dominant and recessive genes. Dominance components exceeded the additive component with the average degree of dominance due to $\sqrt{H_1/D}$ in stomatal density and g_s at both surfaces in all sites and PCI and SSC of the abaxial surface at normal and stress sites and in stress and water holding sites at the adaxial surface which was also greater than unity formulated over-dominance (Table 9). This is in agreement with the results presented by Lamari and Fayt (2015), who found that over-dominance effect for these characters in wheat. In other hand, Khan *et al.* (2011) observed the additive type of gene action with partial dominance for stomatal frequency. The significant value for $H_2/4H_1$ of stomatal density and g_s of both surfaces at all sites confirmed the unequal values of H_1 and H_2 indicated the non-symmetrical distribution of positive and negative genes.

High values of broad-sense heritability (h^2_b) and low to moderate narrow-sense heritability (h^2_n) were observed for all investigated characters (Table 9). The high values of broad-sense and narrow-sense heritability

were observed for stomatal density at stress site by 0.87 and 0.205 respectively. High broad-sense heritability observed for all the traits confirmed that all the traits are more genetic but the role of the additive part is low because of low narrow-sense heritability. These results

imply that the role of the non-additive part is more than additive part (Farshadfar *et al*, 2011). Walton (1974) and Lamari and Fayt (2015) have reported similar findings within the heritability of stomatal density and shape.

Table 5. Mean squares from the diallel analysis for the characters under investigation (Griffing's method 2 model I).

S.O.V	df	Stomatal density						Stomatal shape coefficient (SSC)					
		Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
		Nor.	Str.	W.H.	NOR.	Str.	W.H.	Nor.	Str.	W.H.	NOR.	Str.	W.H.
GCA	7	168**	71**	183**	110**	56**	102**	29.09**	84.03**	16.23**	39.06**	20.15**	17.44**
SCA	28	159**	102**	166**	167**	181**	144**	51.01**	52.68**	77.3**	62.25**	33.83**	51.44**
E'	108	4.02	4.36	3.71	8.28	9.36	7.65	5.60	2.57	4.05	6.16	2.49	2.31
Baker Ratio		0.68	0.58	0.69	0.57	0.38	0.59	0.53	0.76	0.30	0.56	0.54	0.40
S.O.V	df	Potential conductance index (PCI)						Operating stomatal conductance					
		Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
		Nor.	Str.	W.H.	NOR.	Str.	W.H.	Nor.	Str.	W.H.	NOR.	Str.	W.H.
GCA	7	0.0061**	0.0032**	0.0017**	0.0052**	0.0032**	0.001**	0.35**	0.14**	0.11**	0.37**	0.21**	0.04**
SCA	28	0.0102**	0.0029**	0.0051**	0.0152**	0.004**	0.0028**	0.38**	0.17**	0.22**	0.64**	0.33**	0.14**
E'	108	0.0005	0.0003	0.0003	0.0008	0.0003	0.0003	0.0233	0.0098	0.0050	0.0385	0.0150	0.0125
Baker Ratio		0.01	0.09	0.41	0.41	0.61	0.42	0.65	0.61	0.51	0.54	0.56	0.37

* and **: significant at the 5% and 1% probability levels, respectively, ns: non-significant.
Nor.: Normal Irrigations with 85% FC, Str.: Stress Site with 50 % FC, W.H.: water holding at flowering stage

Table 6. Estimates of general combining ability (GCA) of parents for the characters under investigation.

parents	Stomatal density (cnt/mm ²)						Stomatal shape coefficient (SSC)					
	Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
P1	-0.16	-0.21	-0.15	-0.17	-0.02	-0.09	-0.07	-0.10	-0.09	-0.05	0.01	-0.09
P2	0.11	-0.15	0.17	-0.05	-0.07	0.00	0.16	-0.09	0.12	0.24	-0.04	0.11
P3	0.09	0.19	0.07	0.23	0.37	0.23	-0.09	0.03	0.00	0.15	0.06	0.09
P4	0.54	0.34	0.54	0.31	0.06	0.19	0.11	0.35	0.10	-0.05	0.02	0.03
P5	-0.07	-0.14	-0.02	0.37	-0.08	0.38	0.13	0.04	0.06	0.07	-0.13	0.04
P6	0.03	-0.04	0.07	-0.02	-0.23	-0.06	-0.01	-0.10	-0.09	-0.07	0.01	-0.13
P7	-0.05	-0.18	-0.08	-0.01	0.00	-0.03	0.03	0.06	0.04	0.00	0.13	0.03
P8	0.03	0.06	-0.03	-0.10	-0.01	-0.11	-0.13	-0.15	-0.03	-0.02	-0.06	-0.04
Se(gi)	0.06	0.05	0.06	0.06	0.05	0.05	0.03	0.04	0.02	0.03	0.02	0.02
Se(gi-gj)	0.04	0.04	0.04	0.04	0.03	0.03	0.02	0.03	0.02	0.02	0.01	0.02
parents	Potential conductance index (PCI)						Operating stomatal conductance (gs; mol H ₂ O m ⁻² s ⁻¹)					
	Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
P1	-0.001	0.000	0.000	0.000	0.001	0.001	-0.001	-0.003	0.002	0.004	0.005	0.005
P2	0.001	0.001	0.001	-0.002	0.000	0.001	0.000	-0.001	0.005	-0.018	0.002	0.002
P3	0.001	0.001	0.000	0.001	0.001	0.001	0.009	0.007	0.000	0.006	0.010	0.003
P4	0.002	0.000	0.002	0.001	0.000	0.000	0.019	0.004	0.015	0.012	0.002	0.002
P5	-0.002	0.001	0.000	0.002	-0.001	0.001	-0.008	0.002	-0.001	0.020	-0.008	0.015
P6	0.001	-0.001	0.000	0.000	-0.001	-0.001	0.006	-0.006	0.002	0.001	-0.012	-0.004
P7	0.001	-0.001	0.000	0.002	0.001	0.000	0.001	-0.010	-0.002	0.008	0.001	-0.001
P8	0.001	0.000	0.000	0.000	-0.001	0.000	0.004	0.002	0.000	-0.006	-0.004	-0.001
Se(gi)	0.0003	0.0002	0.0002	0.0003	0.0002	0.0002	0.002	0.002	0.001	0.003	0.002	0.002
Se(gi-gj)	0.0002	0.0002	0.0001	0.0002	0.0002	0.0001	0.001	0.001	0.001	0.002	0.001	0.001

Table 7. The estimates of specific combining ability (SCA) of 28 F₁ cross combinations for the characters under investigation.

cross	Stomatal density (cnt/mm ²)						Stomatal shape coefficient (SSC)					
	Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
1×2	-4.96	-5.44	-4.32	-0.96	-3.04	0.48	-1.07	-1.65	0.85	-0.85	-0.45	1.56
1×3	7.04	0.8	7.68	6.88	-2.24	6.4	-1.55	-0.05	-1.69	-5.52	-1.01	-1.62
1×4	3.2	2.24	4.48	0.32	-4.16	0.96	2.07	-5.63	3.37	3.17	-0.5	3.16
1×5	-2.4	3.68	-3.84	-8.48	1.76	-9.28	-0.65	3.79	-2.29	1.53	4.85	-2.5

1×6	-3.52	-2.08	-3.68	4.32	-0.64	3.04	2.05	0.45	2.06	2.87	-0.95	1.15
1×7	3.2	3.36	2.24	8.8	10.88	9.76	-3.57	-0.75	-2.25	-1.75	-2.37	-1.22
1×8	-2.72	-2.4	-2.72	-10.72	-2.4	-11.36	2.73	3.85	-0.05	0.54	0.42	-0.53
2×3	-0.48	-2.72	-1.76	-1.92	-4.48	-0.32	-1.1	-5.67	-2.26	0.06	-4.45	-2.38
2×4	0.32	-1.12	-0.96	0.48	-2.72	1.6	0.22	7.81	-1.13	2.04	2.74	-0.9
2×5	-2.24	8.16	0.64	-1.28	3.84	-1.6	-1.04	0.75	-1.45	-0.97	2.01	-2.58
2×6	3.84	4.8	3.36	-1.44	3.68	-2.88	0.18	-0.43	-1.08	-0.5	2.48	1.28
2×7	-5.6	-6.88	-5.44	2.08	-7.68	-0.32	-2.19	1.55	-3.33	-2.54	1.16	-2.63
2×8	8.96	3.2	8.48	3.2	10.56	2.88	5.45	-2.36	8.41	2.75	-3.49	5.65
3×4	0.32	1.44	0.16	0	7.84	-0.96	-0.98	-3.24	-1.16	-4.76	-1.86	-0.19
3×5	-4.64	-5.12	-4.96	-4	-2.72	-4.32	-0.88	-1.43	-1.81	-3.18	3.17	-1.14
3×6	-1.12	-2.24	-0.96	5.12	-5.76	3.36	0.46	5.46	0.28	-1.13	-0.19	-1.74
3×7	-3.2	-2.88	-2.56	-11.04	-2.08	-10.24	5.11	2.59	6.09	5.07	0.62	7.76
3×8	1.92	10.72	2.24	5.12	9.6	6.08	-1.06	2.34	0.55	9.45	3.71	-0.69
4×5	7.04	1.28	7.68	7.52	6.4	6.88	8.25	3.62	10.46	5.42	0.26	7.22
4×6	2.88	-0.16	3.2	-1.12	-0.48	-2.24	-3.17	-1.18	-2.73	-1.14	-0.08	-0.74
4×7	-8	1.6	-8.64	-3.2	-6.4	-2.24	-1.88	-0.12	-3.35	-0.48	0.06	-3.92
4×8	-5.76	-5.44	-5.92	-4.16	-0.32	-4.16	-4.08	-1.26	-5.46	-4.26	-0.63	-4.63
5×6	-3.52	0.64	-4.32	1.28	3.68	4.64	1.11	-3.11	2.21	1.95	-3.51	1.74
5×7	-0.96	-0.16	-1.28	-3.68	-2.24	-4.48	-3.88	-3.5	-3.72	-1.8	-5.12	-3.08
5×8	6.56	-8.32	6.08	8.48	-10.72	8.16	-2.91	-0.13	-3.41	-2.96	-1.67	0.35
6×7	12.64	0.8	13.28	0.32	6.72	1.6	2.95	0.75	2.95	2.49	3.12	0.78
6×8	-11.2	-1.92	-10.72	-8.48	-7.36	-7.52	-3.59	-1.93	-3.67	-4.55	-0.88	-2.45
7×8	2.08	4.16	2.56	6.56	0.8	5.92	3.45	-0.52	3.62	-0.99	2.52	2.31
Se(sij)	4.8	3.9	4.9	4.9	5.1	4.9	2.74	2.78	3.37	3.05	2.23	2.75
Se(sij-sik)	4.2	3.4	4.3	4.3	4.5	4.3	2.38	2.42	2.93	2.65	1.94	2.39
Potential conductance index (PCI)						Operating stomatal conductance (gs; mol H2O m-2s-1)						
Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface			
cross	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
1×2	-0.046	0.001	-0.029	-0.011	-0.031	0.001	-0.273	-0.066	-0.173	-0.077	-0.363	0.035
1×3	0.072	-0.029	0.034	0.101	-0.012	0.035	0.63	-0.155	0.23	0.85	-0.05	0.184
1×4	0.061	0.021	0.078	0.025	0.008	0.044	0.207	0.328	0.419	-0.088	-0.011	0.178
1×5	-0.019	-0.019	-0.01	-0.052	-0.036	-0.027	-0.07	0.002	-0.027	-0.096	-0.32	-0.155
1×6	-0.048	0.026	-0.027	-0.017	0.03	-0.001	-0.365	0.07	-0.256	-0.152	0.118	0.016
1×7	0.042	0.013	-0.02	0.094	0.042	0.01	0.207	0.022	-0.075	0.541	0.576	0.192
1×8	-0.061	-0.014	-0.025	-0.14	0.000	-0.062	-0.336	-0.203	-0.12	-0.979	0.05	-0.451
2×3	0.05	0.03	-0.02	-0.019	-0.013	-0.013	0.197	0.296	-0.114	-0.152	0.088	-0.067
2×4	-0.112	-0.035	-0.008	0.011	-0.016	-0.009	-0.054	-0.357	-0.011	0.026	-0.178	0.03
2×5	-0.019	0.032	0.017	-0.018	0.025	0.004	-0.11	0.256	0.131	-0.165	0.139	0.034
2×6	0.042	-0.018	0.035	0.018	0.013	0.008	0.308	-0.024	0.19	0.136	0.035	-0.04
2×7	-0.059	-0.024	-0.033	-0.016	-0.041	-0.017	-0.267	-0.278	-0.238	0.062	-0.342	-0.125
2×8	0.046	0.015	0.039	0.035	0.063	0.025	0.2	0.173	0.216	0.17	0.621	0.133
3×4	-0.046	0.007	-0.013	-0.05	0.013	-0.022	-0.204	0.029	0.04	-0.094	0.165	-0.006
3×5	0.003	-0.022	-0.013	0.035	0.026	-0.005	-0.025	-0.125	-0.075	0.117	0.069	-0.069
3×6	-0.018	-0.014	-0.007	0.046	-0.032	0.021	-0.321	-0.235	-0.083	0.173	-0.254	0.149
3×7	-0.043	0.008	0.002	-0.096	-0.007	-0.024	-0.311	-0.011	-0.091	-0.707	-0.152	-0.36
3×8	-0.019	0.02	0.019	-0.016	0.025	0.009	0.032	0.202	0.091	-0.186	0.136	0.168
4×5	0.038	0.036	0.02	0.021	0.005	0.012	0.091	0.04	-0.032	-0.027	0.134	-0.058
4×6	-0.011	-0.032	-0.015	-0.01	-0.032	-0.017	0.331	-0.085	0.005	0.109	-0.096	-0.136
4×7	-0.005	-0.002	-0.031	0.007	0.027	-0.002	-0.12	0.067	-0.285	0.03	0.013	-0.005
4×8	-0.046	0.005	-0.031	-0.005	-0.005	-0.005	-0.066	-0.021	-0.136	0.045	-0.024	-0.003
5×6	-0.054	0.037	-0.018	-0.035	0.002	0.01	-0.3	0.186	-0.157	-0.173	0.123	0.174
5×7	-0.018	-0.029	-0.01	-0.048	-0.016	-0.014	0.036	-0.053	0.038	-0.158	0.046	0.014
5×8	0.07	-0.036	0.015	0.096	-0.022	0.019	0.379	-0.304	0.122	0.502	-0.19	0.059
6×7	0.072	0.012	0.072	0.014	0.029	0.006	0.414	0.093	0.562	-0.154	0.264	0.013
6×8	-0.005	-0.011	-0.038	-0.016	-0.027	-0.027	-0.066	-0.005	-0.262	0.061	-0.187	-0.174
7×8	0.013	0.021	0.02	0.044	-0.033	0.041	0.041	0.158	0.088	0.386	-0.405	0.269
Se(sij)	0.04	0.02	0.03	0.05	0.02	0.02	0.23	0.16	0.18	0.31	0.22	0.15
Se(sij-sik)	0.04	0.02	0.02	0.04	0.02	0.02	0.20	0.14	0.15	0.27	0.19	0.13

Table 8. Mean squares from the Jones diallel analysis for the characters under investigation.

SOV	df	Stomatal density						Stomatal shape coefficient (SSC)					
		Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
		Nor.	Str.	W.H.	NOR.	Str.	W.H.	Nor.	Str.	W.H.	NOR.	Str.	W.H.
a	7	141.1**	219.9**	135**	152.9**	174.7**	130.7**	53.41*	91.28**	29.42ns	45.55ns	24.67*	31**
b	28	177.7**	118.1**	195.5**	190.1**	205.7**	185.2**	44.67**	49.25**	61.51**	59.99**	29.50**	39**
b1	1	1127**	60ns	1292**	1288**	12.1ns	1127**	65.03ns	6.72ns	55.17ns	298**	0.09ns	4.7ns
b2	7	94.8**	173.2**	122.8**	99.7**	305.3**	102.5**	23.65ns	45.55**	17.29ns	16.55ns	21.34**	10ns

	b3	20	159.1**	101.7**	166.1**	166.8**	180.6**	166.9**	51.01**	52.67**	77.30**	63.25ns	33.83**	51**
Error	108	16.08	17.45	14.85	33.1	37.43	30.59	22.41	10.27	16.21	24.64	9.97	9.22	
Potential conductance index (PCI)						Operating stomatal conductance (gs)								
Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface					
SOV	df	Nor.	Str.	W.H.	NOR.	Str.	W.H.	Nor.	Str.	W.H.	NOR.	Str.	W.H.	
a	7	0.004ns	0.002ns	0.002ns	0.006ns	0.003**	0.003*	0.18ns	0.12**	0.1**	0.58**	0.14*	0.21**	
b	28	0.013**	0.003**	0.005**	0.015**	0.004**	0.003**	0.56**	0.19**	0.26**	0.67**	0.33**	0.21**	
b1	1	0.077**	0ns	0.345**	0.776**	0.001ns	0.292**	3.64**	0.07ns	1.89**	2.87**	0.03ns	1.98**	
b2	7	0.01**	0.003**	0.01ns	0.006ns	0.006**	0.002ns	0.56**	0.26**	0.14**	0.42**	0.4**	0.15**	
b3	20	0.01**	0.003**	0.005**	0.015**	0.004**	0.003**	0.38**	0.17**	0.22**	0.64**	0.33**	0.14**	
Error	108	0.002	0.001	0.001	0.003	0.001	0.001	0.093	0.039	0.02	0.154	0.06	0.05	

* significant at the 5%, ** significant at 1% probability levels, respectively, ns: non-significant. a: additive components, b: dominance components, b1: mean square of dominance, b2: mean square of dominance deviation due to arrays, b3: mean square of residual dominance.
Nor.: Normal Irrigations with 85% FC, Str.: Stress Site with 50 % FC, W.H.: water holding at flowering stage

Table 9. Estimation of genetic parameters for the characters under study.

Gen. par.	Stomatal density						Stomatal shape coefficient (SSC)					
	Abaxial surface			Adaxial surface			Abaxial surface			Adaxial surface		
	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.	Nor.	Str.	W.H.
D	13*	76**	14.9*	20.8ns	98.8**	25.4*	6.2ns	6.2ns	3.36ns	-0.87ns	3.8ns	3.7ns
H ₁	163**	129**	182**	161**	229**	162**	31*	31*	51**	39**	25**	34**
H ₂	143**	92**	156**	144**	163**	143**	30**	30**	50**	40**	22**	33**
F	15.4ns	98.9**	23.8ns	23.5ns	157**	32.8ns	4.06ns	4.06ns	2.7ns	-5.34ns	5.09s	2.09ns
E	3.92**	4.48**	3.76**	8.32**	0.69**	7.35**	5.78**	5.78**	4.25**	6.63**	2.60**	2.25**
√(H1/D)	3.54**	1.3**	3.5**	2.78*	1.52**	2.52**	2.23*	2.237*	3.91ns	0ns	2.56ns	3.05*
H ₂ /4H ₁	0.221**	0.178**	0.215**	0.224*	0.178**	0.222*	0.24ns	0.242ns	0.246ns	0.258ns	0.221ns	0.24ns
h _b ²	0.919**	0.87**	0.926**	0.838**	0.863**	0.849**	0.611**	0.611**	0.758**	0.639**	0.713**	0.81**
h _n ²	0.174**	0.205**	0.165**	0.138**	0.074*	0.112**	0.106*	0.106*	0.039ns	0.086ns	0.096*	0.094*
D	0.0017*	0.0004ns	0.0002ns	0.001ns	0.0012*	0.0005ns	0.76ns	0.51*	0.51*	1.21*	0.68*	0.67*
H ₁	0.0117**	0.0029**	0.0041**	0.0128**	0.0046**	0.0025**	5.04**	1.98**	1.98**	5.84**	3.52**	1.65**
H ₂	0.0097**	0.0023**	0.004**	0.012**	0.0034**	0.0024**	3.9**	1.46**	1.46**	5.13**	2.7**	1.4**
F	0.0034*	0.0007ns	0.0001ns	0.0014ns	0.0022*	0.0006ns	1.73*	0.93*	0.93*	1.5ns	1.38*	0.81*
E	0.0005**	0.0002**	0.0002**	0.0007**	0.0002**	0.0003**	0.23**	0.1**	0.1**	0.36**	0.14**	0.13**
√(H1/D)	2.64**	2.87**	4.68ns	3.63ns	1.98**	2.17*	2.57**	2.57**	2.57**	2.57**	2.57**	2.57**
H ₂ /4H ₁	0.21**	0.2**	0.25ns	0.23ns	0.18**	0.24ns	0.19**	0.19**	0.19**	0.19**	0.19**	0.19**
h _b ²	0.85**	0.82**	0.82**	0.83**	0.82**	0.72**	0.82**	0.82**	0.82**	0.82**	0.82**	0.82**
h _n ²	0.06*	0.14**	0.06*	0.06ns	0.09*	0.07ns	0.07*	0.07*	0.07*	0.07*	0.07*	0.07*

* and **: significant at the 5% and 1% probability levels, respectively, ns: non-significant. Gen. para.: genetic parameters, D: additive component of variance, H₁ and H₂: Values of dominant component of variance, F: distribution of dominant and recessive genes, E: environmental component of variance, √(H1/D): average degree of dominance, H₂/4H₁: proportions of genes with positive and negative effects, h_{2b}: broad-sense heritability, h_{2n}: narrow-sense heritability. Nor.: Normal Irrigations with 85% FC, Str.: Stress Site with 50 % FC, W.H.: water holding at flowering stage.

Conclusion: Results revealed a greater amount of genetic variability in wheat genetic material studied indicating better chances for improvement for stomata related characters following selection in later generations. All the traits studied were found to be under control of additive genetic effects along with partial dominance. Due to summary of all morpho-anatomical traits, the Sivand and the Parsi varieties and the Marvdasht×Sivand and the Parsi×Pishtase crosses at normal irrigation regime, the Sivand variety and the Bahar×Pishtase and the Sivand×Pishgam crosses at stress site and the Bahar variety and the Bahar×Pishgam and Parsi×Pishtase crosses at water holding site are the best varieties and crosses for improvement of stomata related characters among other varieties and crosses. Advanced-generation breeding methods were suggested for improvements of stomata related characters under different water regimes. These results will be supportive for future breeding programs aiming to develop drought-tolerant genotypes.

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