

Genetic behaviour for plant capacity to produce chlorophyll in wheat (*Triticum aestivum*) under drought stressMohammad Reza Naroui Rad^{*1,2}, Mihdzar Abdul Kadir¹, Mohd Rafii Yusop³¹Department of Agriculture Technology, Faculty of Agriculture, University Putra Malaysia (UPM), 43400 UPM Serdang, Malaysia²Agriculture and Natural Resources Research Center of Sistan, Iran³Institute of Tropical Agriculture, University Putra Malaysia, 43400 UPM, Serdang, Selangor, Malaysia

*Corresponding author: narouirad@gmail.com

Abstract

The study was conducted with the objective of identifying parents to be used in a breeding program to develop high chlorophyll varieties. Combining ability, heterosis and inheritance of chlorophyll content, including chlorophyll *a*, chlorophyll *b* and total chlorophyll (*a+b*), were investigated in bread wheat obtained from half-diallel crossings among eight parental lines. Cultivars with names of Irena/Babax//Pastor, S-78-11, Tajan, Chamran, Moghan3, Hamoon, Veery/Nacozari and Hirmand have different capacities to produce chlorophyll. Eight parental genotypes and their resulting 28 F₁s were grown in three replications of randomised complete block design. Drought stress was performed with irrigation at 75% soil moisture depletion, the data collected were subjected to analysis of variance and combining abilities were carried out according to Griffing's method 2, model 1. The study was conducted with the objective of identifying parents to be used in a breeding program to develop high chlorophyll varieties. General combining ability and specific combining ability effects were significant for traits' chlorophyll content, chlorophyll *a*, chlorophyll *b* and total chlorophyll; however, non-additive gene effects were predominant over additive effects. The line Irena/Babax//Pastor transmitted high chlorophyll content based on general combining ability to progenies that were made with it. Broad-sense heritabilities were high and strict-sense heritabilities were low for the traits, confirming the importance of non-additive gene effects. This could bring definition of reduced selection efficiency for these mentioned traits.

Keywords: Chlorophyll; Combining ability; Dominance; Gene action; Heritability.**Abbreviations:** GCA-General combining ability; SCA-Specific combining ability; Chl-Chlorophyll; D-additive genetic variance; H1, H2- Dominance genetic variance and corrected dominance genetic variance respectively; E-Environment variance; RCBD - Randomised complete block design; h²(bs)- heritability for diallel in a broad sense; h²(ns)- heritability for diallel in a narrow sense.**Introduction**

Plant breeders collaborate with plant physiologists in order to develop germplasm tolerant to abiotic stress. However, germplasm evaluation is hindered by the difficulty of creating screening methods which are simultaneously accurate and rapid. Drought stress also inhibits the photosynthesis of plants by causing changes in chlorophyll content, affecting chlorophyll components and also damaging the photosynthetic apparatus (Iturbe-Ormaetxe et al., 1998). The decrease in chlorophyll under drought stress is mainly the result of damage to chloroplasts caused by active oxygen species (Smirnoff, 1995). Drought stress also is one of the important factors in limiting plant photosynthesis, causes a large decline in the chlorophyll *a* content, chlorophyll *b* content, and eventually the total chlorophyll content in crops (Manivannan et al., 2007). Chlorophyll is an essential factor in the process of photosynthesis. Chlorophyll *a* and *b* are the two main forms of chlorophyll which contribute to the green-coloured matter in plants. Chlorophyll *a* is yellowish-green whereas chlorophyll *b* is bluish-green. Chlorophyll *a* donates energy directly to the photosynthetic reaction and all other pigments transfer their absorbed energy to it. Chlorophyll *b* and the carotenoids play a key role in protecting the plant

cells against the photochemical reaction induced by the illumination of chlorophyll (Davies et al., 1964). However, a high correlation between the chlorophyll content and photosynthesis rate was not obtained (Marini, 1986). Photosynthetic pigments, and consequently their relationships, are an important indicator of senescence (Brown et al., 1991). Chlorophyll loss is associated with environmental stress and the variation in total chlorophyll/carotenoids ratio may be a good indicator of stress in plants (Hendry and Price, 1993). In addition, measuring gas exchange and chlorophyll content repeatedly on the same leaves in a field may provide useful information on the relationship between these parameters (Schaper and Chacko, 1991). Measurements of chlorophyll fluorescence from photosystem II (PSII) have become a useful method for the determination of mechanisms of photosynthesis and to study the effects of various environmental conditions on photosynthetic reactions (Bolhar-Nordenkamp et al., 1989; Krause, 1991; Demmig-Adams and Adams, 1992). It has been widely considered in research on photosynthesis, stress physiology and crop productivity evaluation (Lichtenthaler, 1988). The specific objective of this study was to estimate the

genetic parameters in an 8×8 half-diallel bread wheat breeding trial to select promising genotypes conferring drought resistance in terms of chlorophyll capacities.

Results

Analysis of variance showed a significant difference for studied traits (Table 2). Phenotypic values of chlorophyll content, chlorophyll *a*, *b* and (*a+b*), differed significantly ($P \leq 0.01$) among the eight parental lines and 28 F₁ hybrids (Table 3). Among the parents, cultivar Irena for chlorophyll content and cultivar Tajan for chlorophyll *a* and (*a+b*) had the highest values respectively (Table 4). Thus, for general combining ability they can be considered as the most photosynthetically efficient cultivars based on their chlorophyll capacities and also, for specific combining ability, cross Moghan3 and Irena/Babax//Pastor has a high value for chlorophyll content (Table 5). Dominance genetic variance considering chlorophyll content was more than other traits (Table 6).

Crosses S-78-11 × Hirmand, Chamran × Veery/ Nacozeni, Irena/Babax//Pastor×Moghan3 and Irena/Babax//Pastor×Tajan produced the most important positive heterosis for chlorophyll content, chlorophyll *a*, *b* and total chlorophyll, respectively (Table 7). This could be due to either epistatic or maternal effects. Both GCA and SCA were highly significant ($P \leq 0.01$) for chlorophyll content, chlorophyll *a* and *b* and total chlorophyll (Table 3). Mean square values were higher for GCA than for SCA of chlorophyll content and chlorophyll *a*, but for chlorophyll *b* and total chlorophyll, the mean square of SCA was higher than what it was for GCA, indicating the importance of both additive and non-additive gene effects. For SPAD, only lines Irena/Babax//Pastor and cultivar Chamran had positive values, demonstrating that they conferred higher chlorophyll content to their progeny. However, cultivar Tajan, Moghan3 and line Veery/Nacozeni could be important to transmit high chlorophyll to their progeny. The highest SCA value for chlorophyll content was obtained by the cross Irena×Moghan3 and for chlorophyll *a*, *b* and chlorophyll *a+b* was obtained by the cross, Irena/Babax//Pastor×Tajan. This indicated the importance of line Irena/Babax//Pastor considering the aspect of transfer of chlorophyll, and also cross Hirmand×S-78-11 had a major effect on chlorophyll content. For all studied characteristics, dominance gene effects (H1, H2) were higher than additive gene ones (Table 6) and this result indicated the dominance control. From the *uv* value it was apparent that the positive and negative alleles at these loci were not in equal proportions in the parental genotypes for all traits. The positive *F* values for all traits indicate an excess of dominant genes for these characters in the parents. The values of average degree of dominance ($H1/D$) 1/2 for all traits were more than one, which suggested the presence of over-dominance in this set of diallel crosses. The ratio (KD/KD+KR) for chlorophyll content showed an equal presence of dominant and recessive genes but for other traits, there was a slight tendency toward dominant genes. The ratio of $hh/H2$ estimates the number of groups which control the character and also exhibit dominance to some degree. These ratios were one grouped gene for all studied traits. The average direction of dominance (*h*) was negative for chlorophyll content, showing that the alleles for chlorophyll content are recessive and the rest are dominant. The proportion of positive and negative genes (*uv*) were unequal, showing different distributions of genes among parents. The

Table 1. Genotype name and pedigree.

No	Pedigree/Name	Tolerance status
1	Irena/Babax//Pastor	Tolerant
2	S-78-11	Tolerant
3	Tajan	Susceptible
4	Chamran	Tolerant
5	Hamoon	Semi-tolerant
6	Moghan3	Susceptible
7	Veery/Nacozeni	Tolerant
8	Hirmand	Semi-tolerant

Table 2. Analysis of variance for traits.

Source of variation	DF	Chlorophyll content	Chl (<i>a</i>)	Chl (<i>b</i>)	Chl (<i>a+b</i>)
Replication	2	5.43	0.029	0.008	0.052
Genotype	35	49.1**	1.407**	0.343**	2.920**
Error	70	6.89	0.06	0.03	0.10

** significant at 1% probability level.

Table 3. Mean squares obtained from analysis variance.

Source of variation	DF	Chlorophyll content	Chl (<i>a</i>)	Chl (<i>b</i>)	Chl (<i>a+b</i>)
Replication	2	92.49	0.02	0.01	0.06
GCA	7	64.59**	1.66**	0.27**	2.98**
SCA	28	36.65**	1.29**	0.37**	3.09**
Error	70	5.42	0.04	0.02	0.09

GCA, general combining ability; SCA, specific combining ability. ** significant at 1% probability level

uv component ranged from 0.20 for chlorophyll *a* to 0.23 for chlorophyll content. The high broad sense heritability was obtained for almost all the traits studied. The high broad sense heritability ranged from 78% for chlorophyll content to 96% for chlorophyll *a*, but for narrow sense heritability the values reduced and ranged from 0.13 to 0.24. The low values of narrow sense heritability are due to a more non-additive proportion than additive.

Discussion

The concept of combining ability refers to the capacity or ability of a genotype to transmit superior performance to its crosses. To mitigate the impact of water stress, plants use different strategies such as morphological, anatomical and physiological mechanisms to reduce transpiration, improve water absorption and limit oxidative damage. Chlorophyll concentration has been known as an index for evaluation of source (Herzog, 1986) therefore, a decrease of this can be considered as a non-stomata limiting factor in the drought stress conditions. The variation exhibited by the 4 characters under consideration (Table 1) indicated that selection for some of these drought-related characters could be effective in developing drought-tolerant cultivars. Although selection of the characters studied may be effective in improving drought-tolerant cultivars, the selection efficiency is related to the magnitude of heritability. There are reports about the decrease of chlorophyll in drought stress conditions (Majumdar et al., 1991; Mayoral et al., 1981; Kuroda et al., 1990). Also, it is reported that the chlorophyll content of resistant and sensitive cultivars to drought and thermal stress is reduced. However, resistant cultivars to drought and thermal stress conditions had a high chlorophyll content

Table 4. Values of general combining ability (GCA) of chlorophyll content (SPAD), chl(*a*), chl(*b*) and chl(*a+b*) the parental lines in F₁ generation

Cultivar/line	Chlorophyll content	Chl(<i>a</i>)	Chl(<i>b</i>)	Chl(<i>a+b</i>)
Irena/Babax//Pastor	3.31**	-0.14	-0.09	-0.23*
S-78-11	-0.98	-0.36**	-0.06	-0.42**
Tajan	-0.73	0.48**	0.16**	0.64**
Chamran	1.56*	-0.29**	-0.22**	-0.51**
Hamoon	0.57	-0.13	0.02	-0.11
Moghan3	-3.07**	0.28**	0.01	0.29**
Veery/Nacozari	-0.72	0.26**	0.14**	0.40**
Hirmand	0.05	-0.10	0.04	-0.06

SE (g_i) chlorophyll content = 0.76, SE (g_i) chlorophyll *a* = 0.072, SE (g_i) chlorophyll *b* = 0.051, SE (g_i) chlorophyll (*a* + *b*) = 0.093 , *and ** significant at 5% and 1% probability level

Table 5. Values of SCA of chlorophyll content, chlorophyll *a*, *b* and chlorophyll (*a+b*)

Crosses	S-78-11	Tajan	Chamran	Hamoon	Moghan3	Veery/Nacozari	Hirmand
Irena/Babax//Pastor Chl (C)*	-3.8	0.26	-0.02	-0.64	3.90	3.75	-3.38
Chl (<i>a</i>)	0.48*	1.27**	0.24	-0.59**	0.42	-1.21	-0.60**
Chl (<i>b</i>)	-0.03	0.66**	0.04	-0.24	0.33*	-0.57**	-0.20
Chl (<i>a+b</i>)	0.45	1.93	0.28	-0.83**	0.75**	-1.77	-0.80**
S-78-11 Chl (C)		-4.88*	2.10	-5.65*	3.35	1.34	3.60
Chl (<i>a</i>)		-0.72**	-0.35	0.08	-0.61**	0.65**	0.47*
Chl (<i>b</i>)		-0.48**	-0.02	-0.17	-0.18	0.35*	0.52**
Chl (<i>a+b</i>)		-1.19**	-0.37	-0.09	-0.79**	1**	1**
Tajan Chl (C)			-0.58	1.40	1.10	-0.68	3.39
Chl (<i>a</i>)			-1.19	-0.21	0.29	-0.19	0.75**
Chl (<i>b</i>)			-0.53**	0.09	-0.03	-0.08	0.36*
Chl (<i>a+b</i>)			-1.72**	-0.12	0.26	-0.28	1.11**
Chamran Chl (C)				1.42	-1.71	1	-2.20
Chl (<i>a</i>)				0.36	0.56*	0.39	0.1
Chl (<i>b</i>)				0.24	0.38*	0.03	-0.15
Chl (<i>a+b</i>)				0.60*	0.94**	0.42	-0.15
Hamoon Chl (C)					1.37	2.69	-0.58
Chl (<i>a</i>)					-0.03	0.75**	-0.35
Chl (<i>b</i>)					-0.10	0.42**	-0.25
Chl (<i>a+b</i>)					-0.13	1.17**	-0.60*
Moghan3 Chl (C)						-5.64*	-2.37
Chl (<i>a</i>)						-0.36	-0.26
Chl (<i>b</i>)						-0.14	-0.27
Chl (<i>a+b</i>)						-0.50	-0.53
Veery/Nacozari Chl (C)							-2.46
Chl (<i>a</i>)							-0.10
Chl (<i>b</i>)							-0.01
Chl (<i>a+b</i>)							-0.04

*Chlorophyll content, SE (s_{ij}) chlorophyll content = 2.34, SE (s_{ij}) chlorophyll *a* = 0.22, SE (s_{ij}) chlorophyll *b* = 0.15, SE (s_{ij})C chlorophyll (*a* + *b*) = 0.28, *and ** significant at 5% and 1% probability levels, respectively.

(Sairam et al., 2002). Other reports have represented that drought stress did not have an effect on chlorophyll concentration (Kulshreshtha et al., 1987). Pastori and Trippi (1993) expressed that resistant genotypes of wheat and corn had higher chlorophyll content than sensitive genotypes under the oxidative stress. Griffing (1956) type analysis showed that mainly non-additive genes controlled the two studied traits. The general combining ability values of parental lines showed that cultivar Tajan generally transmitted high chlorophyll *a*, *b* and (*a+b*) to its progenies and line Irena/Babax//Pastor for chlorophyll content, whereas cultivar Moghan3 transmitted low chlorophyll content (susceptibility to drought). According to Hayman (1954) and Jinks (1954) analysis, these additional genes of resistances were dominant. Based on comparison of MP values, F₁

hybrids Irena/Babax//Pastor×Hamoon and S-78-11×Hamoon showed lower values for all traits than both parents. This was also confirmed by some negative values of SCA, indicating either the existence of different genes with minor effects in each line or interaction between resistance genes. Abd et al.'s (2009) research showed highly significant positive general combining ability effects for chlorophyll content. Hayman (1954) and Jinks' (1954) type analysis showed a significant dominance effect for all studied characters. In general, the results of Griffing (1956) type analysis corroborated those of Hayman (1954) and Jinks (1954). Genetic analysis (Table 6) demonstrated that these four characters are predominantly controlled by dominant gene action; it appears that selection for them cannot be done in the F₁ generation. Farshadfar et al. (2011) reported that chlorophyll fluorescence was controlled

Table 6. Genetics parameters of Hayman type analysis for chlorophyll content, chlorophyll(a), chlorophyll(b) and chlorophyll (a+b).

Genetic Parameters	Chlorophyll content		Chl (a)		Chl (b)		Chl (a+b)	
	Mean	Heterosis	Mean	Heterosis	Mean	Heterosis	Mean	Heterosis
D	10.18		0.39		0.03		0.67	
H1	36.73		1.88		0.46		4.10	
H2	34.22		1.55		0.42		3.48	
F	1.34		0.46		0.04		0.85	
hh	-0.71		0.05		0.17		0.41	
E	3.88		0.02		0.008		0.03	
(H1/D) ^{1/2}	1.89		2.18		3.63		2.46	
KD/KD+KR	0.51		0.63		0.57		0.62	
hh/H2	-0.02		0.03		0.47		0.13	
H	-0.93		0.24		0.42		0.62	
uv	0.23		0.20		0.22		0.21	
h ² (bs)	0.78		0.96		0.93		0.95	
h ² (ns)	0.13		0.24		0.13		0.19	

D: additive genetic variance, H1 and H2: dominance genetic variance and: corrected dominance genetic variance, F: product of additive by dominance, hh: square of difference P vs. All, E: Expected environmental variance, whole, (H1/D)^{1/2}: average of degree dominance, KD/KD+KR: proportion of dominance genes, hh/H2: number of effective factors, h: average direction of dominance, uv: balance of positive and negative alleles, h²(bs): heritability for diallel in a broad sense, h²(ns): heritability for diallel in a narrow sense

Table 7. Phenotypic values of chlorophyll content (SPAD), chlorophyll a, chlorophyll b and chlorophyll (a+b) of the eight parental lines and the 28 F₁ hybrids.

Parent/Crosses	Chlorophyll content		Chl (a)		Chl (b)		Chl (a+b)	
	Mean	Heterosis	Mean	Heterosis	Mean	Heterosis	Mean	Heterosis
1	40.3		1.88		1.53		2.67	
2	33		1.23		1.01		1.96	
3	35.6		2.59		2.12		3.5	
4	38.1		1.71		1.40		2.5	
5	37.13		2.78		2.26		4.11	
6	32.7		2.13		1.82		2.76	
7	34.06		1.14		0.97		1.81	
8	38.23		2.72		2.18		3.82	
1×2	32.83	-10.41	2.14	37.62	1.68	20.86	3.06	32.08
1×3	37.2	-1.97	3.77	68.82	3.01	11.23	4.61	81.65
1×4	39.2	0.006	1.96	9.56	1.62	5.88	2.80	8.43
1×5	37.6	-2.88	1.3	-44.20	1.16	-25.19	2.09	-38.24
1×6	38.5	5.47	2.72	35.82	2.29	88.37	4.07	49.66
1×7	40.7	9.45	1.08	-28.55	0.88	-20.18	1.66	-25.81
1×8	34.33	-12.56	1.32	-42.40	1.16	-9.347	2.18	-32.78
2×3	27.76	-19.04	1.56	-18.32	1.32	-10.52	2.29	-15.97
2×4	37.03	4.17	1.153	-21.54	1.03	5.67	1.96	-12.23
2×5	28.33	-19.20	1.75	-12.71	1.47	-13.04	2.65	-12.82
2×6	33.66	2.48	1.476	-12.10	1.49	25.72	2.34	-1.12
2×7	34	1.391	2.71	12.93	2.40	16.54	4.24	12.31
2×8	41.03	15.20	2.17	10.025	1.82	75.59	3.78	30.76
3×4	34.6	-6.10	1.16	-45.89	1.01	-39.21	1.68	-44
3×5	35.6	-2.10	2.30	-14.09	1.86	22.73	3.68	-3.23
3×6	31.66	-7.27	3.21	36.15	2.66	60.34	4.45	42.12
3×7	32.23	-7.46	2.71	45.35	2.2	66.73	4.03	51.72
3×8	37.06	0.406	3.29	24.01	2.67	66.38	4.96	35.61
4×5	37.9	0.75	2.09	-6.607	1.71	8.63	3.25	-1.71
4×6	31.13	-12.05	2.71	41.14	2.21	78.50	3.98	51.26
4×7	36.2	0.32	2.52	76.86	2.13	44.87	3.58	66.02
4×8	33.76	-11.52	1.773	-20.06	1.46	-17.52	2.55	-19.30
5×6	33.23	-4.8	2.28	-6.99	1.95	4.90	3.31	-3.58
5×7	36.9	3.65	3.04	55.14	2.51	68.43	4.73	59.64
5×8	34.4	-8.71	1.58	-42.49	1.32	-24.72	2.49	-37.05
6×7	24.93	-25.31	2.35	43.78	1.98	67.93	3.45	50.69
6×8	28.96	-18.32	2.09	-13.79	1.70	0.96	2.96	-9.91
7×8	31.23	-13.60	2.30	19.03	1.96	43.77	3.57	26.78

by additive type of gene action. According to Hayman (1954), this may lead to overestimation or underestimation of some parameters (dominance and epistasis). Additionally, because of the low values of narrow sense heritability mainly for all traits, the selection based on chlorophyll will be less efficient and genetic gain will be less important. Similarly, there was a report of high broad sense heritability for chlorophyll *a* and *b* in wheat (Zhang et al., 2009). Chlorophyll capacity can be much more important in conferring resistance to drought due to obvious difficulty in screening large numbers of plants; one way is to use molecular markers, which can greatly enhance the efficiency of breeding for improved water uptake (Lynch., 1995), quantitative trait loci linked to drought resistance traits can be another way for identifying high-yielding wheat cultivars suitable for regions with limited water conditions.

Materials and methods

Plant Materials

Eight bread wheat cultivars were used as parents (Table 1). Parental genotypes were derived from seed and plant improvement institute, Karaj-Iran, and tolerance status was determined from preliminary and advance experiments in this institute. Crosses for a half-diallel among these wheats were made in the Agriculture and Natural Resources Research Center of Sistan-Iran. F₁ hybrids and their parents were planted under shelter in pots.

Trial

In the season (2010–11), the 28 F₁ hybrids and their eight parents were sown in plastic pots filled with a soil mixture containing soil/sand/organic matter in a ratio of 1:1:1 in Experiments Farm of University Putra Malaysia. Four seeds were sown in each pot. The pots were irrigated after 75% depletion of the soil water. Each pot was filled with 3 kg of air-dried soil and soil field capacity was calculated on the soil dry weight basis. Water stress treatments were 75% of moisture depletion of field capacity by weight. The pots were weighed at two days intervals to compensate the water loss by evapotranspiration and irrigation was performed after 75% depletion of field capacity of soil and genotypes were arranged as a completely randomised block design. The chlorophyll content was measured 3 times. Measurements were made on the flag leaf on two seedlings per pot, with a chlorophyll meter, (SPAD-502, Soil Plant Analysis Development (SPAD) Section, Minolta Camera Co, Osaka, Japan). Three readings were taken along the middle section of the leaf, and the mean was used for analysis and values were expressed as SPAD units. Chlorophyll *a* and *b* were estimated by extracting the leaf material in 80% acetone. Absorbances were recorded at 645, 665 and 470 nm for chlorophyll *a* and *b* respectively, and finally total chlorophyll (*a+b*) was calculated based on Arnon's procedure, 1949.

Statistical and genetic analysis

All data were subjected to analysis of variance. Data obtained from the 28 hybrids of F₁ and eight parents were subjected to a Jinks–Hayman type diallel analysis for genetic parameters (Hayman, 1954; Jinks, 1954) and analysed by Griffing's method II, model 1. To investigate relative performance of parent lines and heterosis in the F₁, midparent (MP) heterosis was calculated over blocks using the formula (F₁-MP)/MP (Halluerm and Miranda, 1981). The narrow-sense and broad-

sense degrees of heritability were calculated according to the method suggested by Mather and Jinks (1982). The analysis was performed using the DIAL98 software (Yukai, 1989).

Conclusion

For chlorophyll content and chlorophyll *a*, general combining ability (GCA) and specific combining ability (SCA) were highly significant, but GCA had a more significant effect than SCA, indicating the importance of additive effects of genes compared to interaction effects (dominance and epistasis). The line Irena/Babax/Pastor had a high GCA value for chlorophyll content and also cultivar Tajan for chlorophyll *a* and (*a+b*) Therefore, these lines were recommend as a source of chlorophyll for making crosses. Finally, genetic gain per cycle of selection in preliminary generations will be less for chlorophyll due to low narrow sense heritability and dominance effect for traits studied.

References

- Abd Allah AA, Mohamed AAA, Gaballah MM (2009) Genetic studies of some physiological and shoot characters in relation to drought tolerance in rice. *Journal Agric Res* 4: 964-990.
- Arnon DI (1949) Copper enzymes in isolated chloroplast polyphenol oxidase in *Beta vulgaris*. *Plant Phys* 24:1–15.
- Bolhar-Nordenkamp HR, Long SP, Baker NR (1989) Chlorophyll fluorescence as a probe of the synthetic competence of leaves in the field: a review of current instrumentation. *Func Ecology* 3:497-514.
- Brown SB, Houghton JD, Hendry GAF (1991) Chlorophyll breakdown. In: Scheer, H (Ed.), *Chlorophylls*. CRC Press, Boca Raton. 465–489.
- Davies DD, Giovanelli J, Rees T (1964) *Plant biochemistry*. Blackwell Scientific Publications, Oxford. UK
- Demmig-Adams B, Adams II (1992) Photo protection and other responses of plants to high light stress. *Annu Rev Plant Physiol Plant Mol Bio* 43:599-626.
- Farshadfar E, Valiollah R, Jaime Teixeira D, Farshadfar M (2011) Inheritance of drought tolerance indicators in bread wheat (*Triticum aestivum* L.) using a diallel technique. *Aust J Crop Sci* 5(3): 308-317
- Griffing B (1956a) Concept of general and specific combining ability in relation to diallel crossing systems. *Aust J Bio Sci* 9:463-493
- Hendry GAF, Price AH (1993) *Methods in comparative plant ecology*. Chapman and Hall, London. 148-152.
- Halluerm AR, Miranda JB (1981) *Quantitative Genetics in Maize Breeding*. Ames, IA: Iowa State University Press.
- Hayman BI (1954) The analysis of variance of diallel tables. *Biometrics* 10: 235-244.
- Herzog H (1986) *Source and sink during reproductive period of wheat*. Scientific publishers. Berlin and Hamburg. 147-148.
- Iturbe-Ormaetxe I, Escuredo PR, Arrese-Igor C, Becana M (1998) Oxidative damage in pea plants exposed to water deficit or paraquat. *Plant Physiol* 116: 173–181.
- Jinks JL (1954) The analysis of continuous variation in diallel crosses of *Nicotiana rustica* varieties. *Genetics* 39:767–788.
- Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: the basis. *Annu Rev Plant Physiol Plant Molec Biol* 313-349.

- Kulshreshtha SDP, Mishra R, Gupta K (1987) Changes in contents of chlorophyll, proteins and lipids in whole chloroplast and chloroplast membrane fractions at different leaf water potentials in drought resistant and sensitive genotype of wheat. *Photosynthetica* 21:65-70.
- Kuroda M T, Imagawa H (1990) Changes in chloroplast peroxidase activities in relation to chlorophyll loss in barley leaf segments. *Physiol Planta* 80:555-560.
- Lynch JP (1995) Root architecture and plant productivity. *Plant Physiol* 109:7-13.
- Lichtenthaler HK, Buschmann C, Rinderle U, Schmuck G (1988) Application of chlorophyll fluorescence in ecophysiology. *Environ. Biophys* 25(297):308.
- Majumdar S, Ghosh S, Glick BR, Dumbroff EB (1991) Activities of chlorophyllase, phosphoenolpyruvate carboxylase and ribulose-1,5-bisphosphate carboxylase in the primary leaves of soybean during senescence and drought. *Physiol Planta* 81:473-480.
- Manivannan P, Abdul Jaleel C, Sankar B, Kishorekumar A, Somasundaram, Lakshmanan GMA, Panneerselvam R (2007) Growth, Biochemical modifications and proline metabolism in *Helianthus annuus* L. as induced by drought stress. *Colloids and Surfaces B: Biointerfaces* 59:141-149.
- Marini RP (1986) Do net gas exchange rates of green and red peach leaves differ. *Hort Sci* 21: 118-120.
- Mather K, Jinks J L (1982) *Biometrical Genetics: The Study of Continuous Variation*. 3rd edn. New York, Chapman and Hall Publishers.
- Mayoral MLD, Shimshi D, Gromete- Elhanan Z (1981) Effect of water stress on enzyme activities in wheat and related wild species: carboxylase activity, electron transport and photophosphorylation in isolated chloroplasts. *Aust J Plant Physiol* 8:385-393.
- Pastori GM, Trippi VS (1993) Cross resistance between water and oxidative stress in wheat leaves. *J Agric Sci* 120:289-294.
- Sairam RK, Siravastava GC (2002) Changes in antioxidant activity in subcellular fractions of tolerant and susceptible wheat genotypes in response to long term salt stress. *Plant Sci.* 162:897-907.
- Schaper H, Chacko EK (1991) Relation between extractable chlorophyll and portable chlorophyll meter readings in leaves of eight tropical and subtropical fruit tree species. *J Plant Physiol* 138: 674-677.
- Smirnoff N (1995) Antioxidant systems and plant response to the environment. In: Smirnoff 5th Edn, BIOS Scientific Publishers, Oxford, UK.
- Yukai Y (1989) A microcomputer program diall for diallel analysis of quantitative characters. *Jpn J Breed* 39:107-109.
- Zhang K, Zhang Y, Chen G, Tian J (2009) Genetic Analysis of Grain Yield and Leaf Chlorophyll Content in Common Wheat . *Cereal Res Communications* 37:499-511.