Pak. j. sci. ind. res., vol. 36, no. 8, August 1993

PHYSIO-GENETIC BASIS FOR DROUGHT TOLERANCE IN SPRING WHEAT

MUHAMMAD ASLAM CHOWDHRY, RASHID HUSSAIN, IHSAN KHALIQ AND NAEEM MAHMOOD
Department of Plant Breeding & Genetics, University of Agriculture, Faisalabad, Pakistan

(Received November 12, 1992; revised May 2, 1993)

Nine wheat genotypes (6 females and 3 males) were crossed in the crop season 1989-90. Data on some drought related and yield characters were recorded and subjected to combining ability studies. Cross LU26S x HABA 3 indicated positive GCA effects for osmotic pressure, stomatal size and yield characters. While the crosses HABA 3 x LU26S, HABA 4 x Pak.81 and LABA 3 x LU26S showed positive SCA effects for grain yield. These crosses may prove useful in future breeding.

Key words: Wheat genotype, Combining ability, Drought.

Introduction

Wheat employs a pivotal position in Pakistan's economy occupying the largest area with the highest production. About one third of wheat sown area in the country depends exclusively on winter rains which are uneven in distribution. Therefore a substantial area of wheat crop is under constant moisture stress during crucial periods of its growth and development. Physiological and morphological adaptations to moisture stress include increased ABA (abscisic acid), changes in stomatal size and number and high osmotic pressure. ABA, a growth hormone, can play very important role by reducing the water requirements of the plants as high endogenous levels of ABA cause the closure of stomata thus reducing the rate of transpiration. It is now generally accepted that, in most plants, an increase in the level of endogenous ABA follows the onset of water stress plant [1]. In many plants there is a good correlation between the build up of ABA and the closure of stomata stimulated by water stress. In some cases, however, stomata begin to close before the level of ABA in the plant has risen appreciably [2]. Further ABA also enhances the growth rate thus enabling the plant to complete its life-cycle before a serious moisture deficit develops. The number of stomata on upper and lower surfaces of wheat leaves was higher in dry soil than in irrigated conditions [3]. High osmotic pressure is considered to be the main reason for desert plants to resist drought as this enables the plants to develop a high suction force to absorb the available soil moisture more rapidly [4]. Wheat cultivars contain varying amounts of carbohydrates. Varieties growing in droughty environments have low proportion of carbohydrates as compared to those sown in irrigated areas. This is due to inadequate supply of water at the time of grain filling period, seed is invariably shrivelled and low weightage due to reduced carbohydrate contents.

In a line x tester analysis of combining ability, non additive gene action occurred for grain yield per plant, number of ear bearing tillers and synchrony of tillering, while additive gene action controlled early growth vigour, days to heading and plant height [5]. Plant height, spike length, spikelets per spike and grains per spike were mainly controlled by additive gene effects whereas gene action was non-additive for 1000-grain weight and grain yield per plant [6-11]. In general, performance of a parent was closely related to its general combing ability. The present studies, therefore, were planned to comprehend the genetic nature and relative contribution to general and specific combining ability of related cultivars/lines as a means of selecting parents for hybridization.

Materials and Methods

Six lines of wheat, namely High ABA 3, High ABA 4, High ABA 6, Low ABA 3, Low ABA 4, Low ABA 6 (female parents), an two varieties and one line, Pak.81, LU26S and K-1595 (male parents/testers), were crossed in the crop season 1989-90. Seeds of F_1's including parents were sown in the field in a triplicated randomized complete block design in Nov. 1990. Data from ten guarded plants per plot were recorded on the following drought related morpho-physiological plant parameters.

Osmotic pressure (m osm kg^{-1}). Fresh and turgid third nodal leaves were collected in the early morning hours in small polythene bags. Leaf samples were then stored in a deep freezer for three days till cell wall breakage. Tissue sap was extracted and centrifuged at 6500 RPM for 10 minutes. Ten micro liters of this sap sample were used to determine osmotic pressure by using automatic micro-osmometer.

Stomatal frequency and stomatal size (m^2). Leaf strips of about 3 cm length were taken from the midle part of third nodal leave, dipped into Carnoy's solution to arrest stomatal structure and remove chlorophyll. After washing with alcohol samples were examined under the microscope at 10x magnifications to count number of stomata and at 40x magnifications to measure size of stomatal opening, by using a stage micrometer (scaled at 0.01 mm increments) and an ocular micrometer (scaled at 0.1 mm increments).

Carbohydrate (%age). Protein, fat, ash and fiber percentage were determined by standard method of AACC (1976) and carbohydrates other than crude fiber by difference.

In addition, data on some yield parameters were also recorded. The data were subjected to analysis of variance technique [10]. Combining ability studies were made by using line x tester analysis [13].

Results and Discussion

Differences among genotypes were highly significant except for stomatal size and grain yield (Table 1). Analysis of parents and crosses depicted highly significant differences among parents for days to heading, osmotic pressure, 100-grain weight and carbohydrates. Highly significant differences were found among crosses for all the characters except stomatal size and grain yield. Variation due to parents x crosses was highly significant for days to heading, osmotic pressure and carbohydrates.

Line x tester analysis of variance revealed highly significant differences among lines (females) for days to heading and significant differences for 1000-grain weight and carbohydrates whereas highly significant differences for days to heading and 1000-grain weight and significant differences for carbohydrates were observed among testers (males). Variation due to line x tester interaction was highly significant for days to heading, osmotic pressure, and stomatal frequency.

Mean performance of parents and crosses. The male and female parents used provided broad range of expression for various characters studied (Table 2). Considerable degree of hybrid vigour existed in most of the crosses for majority of the characters studied. Some hybrids even exceeded their better parents. However, some intermediate hybrids and some decreasing in favour of lower parent were also observed. Mean performance of crosses is presented in Table 3.

COMBINING ABILITY STUDIES

(a) General combining ability effects. Estimates of variation due to general combining ability were partitioned into male and female parents for different plant traits to search out potential for subsequent breeding.

In case of days to heading, those genotypes are required which can complete their heading in a short span. Therefore negative effects are given more importance.

Under moisture deficit conditions only those genotypes will survive which can maintain high osmotic pressure in their tissues. Among males, the highest GCA effects were exhibited by variety LU26S. Among females, the line HABA 4 was the best general combiner. Plants with higher number and smaller size of stomata can better tolerate the moisture deficiency as they can efficiently and economically regulate the supply of water but reducing the rate of transpiration. As a result, the photosynthetic capacity of the plant is enhanced thus ultimately increasing the final grain yield. As regards stomatal frequency, variety LU26S was the best general combiner. In case of stomatal size, negative effects are given more importance. From this point of view, male parent Pak. 81 and female parent LABA 6, LABA 3 and LABA 4 were found to be the potential parents. On the basis of the requirements for more grain weight, several parents viz., HABA 3, HABA 4, HABA 6 and tester line K-1595 can be potential parents to breed for higher 1000-grain weight.

The GCA effects for grain yield were of low magnitude. Only four of the nine parents demonstrated positive GCA effects. Among testers variety LU26S exhibited higher GCA effects whereas line LABA 3 displayed highest GCA effects among females.

Generally a variety growing under moisture stress conditions, contains very low proportions of carbohydrates, ultimately leading to lower grain yield. This is due to the reason

TABLE 1. ANALYSIS OF VARIANCE OF SOME MORPHO-PHYSIOLOGICAL CHARACTERS OF WHEAT GENOTYPES DERIVED FROM LINE X TESTER ANALYSIS OF SIX LINES AND THREE TESTERS.

Source of variation	Degree of freedom	Days to heading	Osmotic pressure (m osm/kg)	Stomatal frequency	Stomatal size (μm²)	1000-grain weight (g)	Carbohydrates (%age)	Grain yield per plant (g)
Replications	2	4.3087^{NS}	230.778^{NS}	0.3796^{NS}	8587.52^{NS}	2.0717^{NS}	0.5013^{NS}	11.3362^{NS}
Genotypes	26	75.4568**	12901.368**	1.0297**	4197.59^{NS}	60.6456**	2.9089**	17.5293^{NS}
Parents	8	115.9815**	8471.537**	0.5241^{NS}	4634.45^{NS}	106.0107**	3.5392**	23.2192^{NS}
P vc C	1	90.3765**	11300.061**	0.0860^{NS}	23346.03^{NS}	312.6389**	13.5952**	65.4621^{NS}
Crosses	17	55.5087**	15080.188**	1.3231**	2865.63^{NS}	24.4741**	1.9837**	12.0321^{NS}
Lines	5	93.3630**	18596.774^{NS}	1.5865^{NS}	191.91^{NS}	36.8404*	3.1688*	10.9118^{NS}
Testers	2	201.9074**	34783.462^{NS}	0.1135^{NS}	4962.78^{NS}	83.1527**	4.9420*	1.3241^{NS}
L x T	10	7.3519**	9381.241**	1.4333**	3783.06^{NS}	6.5553^{NS}	0.7996^{NS}	14.7339^{NS}
Error	52	1.5266	621.662	0.4297	6392.190	4.1067	0.5245	18.4361

*, **, NS = Significant at 0.5 and 0.1% level of significance and non-significant, respectively.

that under deficit conditions, seed is invariably shrivelled and reduced in weightage due to inadequate supply of water at the time of grain filling. Only five of the nine parents manifested positive GCA effects for carbohydrates. Line K-1595 displayed highest GCA effects among testers followed by variety LU26S whereas among females highest GCA effects were exhibited by line HABA 3, followed by HABA 4 and HABA 6.

(b) Specific combining ability effects. If early heading varieties can perform better under drought atmosphere, then crosses viz., HABA 4 x Pak. 81, LABA 4 x K-1595 and LABA 6 x K-1595 are the best specific combinations. SCA effects were positive in 7 of the crosses for osmotic pressure. Crosses worth mentioning were LABA 3 x K-1595, HABA 3 x LU26S,

TABLE 2. MEAN VALUES FOR ALL THE CHARACTERS STUDIED OF 6 FEMALES AND 3 MALES.

Parents	Days to heading	Osmotic pressure (m osm/kg)	Stomatal frequency	Stomatal size (µm²)	1000-grain weight (g)	Carbohydrates (%age)	Grain yield per plant (g)
Males							
1. Pak. 81	111.33c	408.33b	4.40	884.84	36.00a	72.27b	24.01
2. K-1595	103.00b	162.00a	5.20	903.05	38.73a	70.96a	23.64
3. LU 26S	99.67a	546.00c	5.38	932.55	44.33b	72.05ab	23.63
Females							
1. High ABA 3	103.00a	468.67d	5.80	899.53	34.00c	69.86bc	20.81
2. High ABA 4	101.67a	436.67cd	5.40	919.69	35.40c	70.10c	18.86
3. High ABA 6	101.67a	374.00a	5.62	854.90	35.07c	69.96bc	19.87
4. Low ABA 3	114.00b	380.33ab	4.98	905.65	29.45b	69.50abc	18.68
5. Low ABA 4	113.33b	407.00abc	4.93	997.89	24.93a	68.36a	15.68
6. Low ABA 6	114.67b	420.33bc	5.40	928.22	27.40ab	68.90ab	20.10
$LSD_{0.05}$	2.03	40.89	NS	NS	3.31	1.18	NS

TABLE 3. MEAN PERFORMANCE OF CROSSES

Crosses	Days to heading	Osmotic pressure (m osm/kg)	Stomatal frequency	Stomatal size (µm²)	1000-grain weight (g)	Carbohydrates (%age)	Grain yield per plant (g)
High ABA 3 x Pak. 81	104.67f	409.33bc	5.03abcd	968.68	39.00cde	71.27cde	20.19
High ABA 3 x K-1595	99.00ab	420.67c	4.80abcd	971.65	41.87ef	71.80ef	25.02
High ABA 3 x LU26S	102.00cde	595.67h	5.20abcd	938.78	40.07de	71.45def	25.35
High ABA 4 x Pak. 81	101.67cd	468.33d	4.87abcd	943.23	36.47bc	70.48bcd	24.49
High ABA 4 x K-1595	98.67a	536.00fg	5.67cdef	960.20	44.80f	72.56f	21.75
High ABA 4 x LU26S	102.67cdef	541.33fg	5.27abcde	950.49	39.27cde	71.28cde	20.92
High ABA 6 x Pak. 81	104.00ef	388.33abc	5.53bcdef	914.24	38.20cd	70.35bcd	22.78
High ABA 6 x K-1595	101.00bc	379.67ab	4.20a	921.67	39.47cde	71.50def	21.32
High ABA 6 x LU26S	103.33def	392.00abc	4.93abcdl	010.02	39.07cde	71.19cde	20.76
Low ABA 3 x Pak. 81	109.33gh	387.00abc	4.60abc	968.92	34.73ab	70.10abc	23.46
Low ABA 3 x K-1595	101.00bc	566.00gh	6.40f	954.19	38.63cde	70.66bcde	21.80
Low ABA 3 x LU26S	107.67g	477.00de	5.77def	919.65	38.97cde	71.20cde	26.48
Low ABA 4 x Pak. 81	111.67i	362.00a	4.93abcd	892.33	33.07a	69.02a	20.85
Low ABA 4 x K-1595	102.67cdef	397.33abc	5.73def	966.92	38.80cde	71.08bcde	19.48
Low ABA 4 x LU26S	110.00hi	516.00ef	4.53ab	986.06	36.27abc	70.47bcd	22.81
Low ABA 6 x Pak. 81	112.00i	462.00d	6.33ef	912.77	34.38ab	70.33bcd	23.23
Low ABA 6 x K-1595	103.00cdef	478.33de	5.13abcd	933.09	38.07cd	70.16abc	23.79
Low ABA 6 x LU26S	110.00hi	480.67de	6.53f	991.03	34.53ab	69.97ab	20.13
$LSD_{0.05}$	2.03	40.89	1.08	NS	3.31	1.18	NS

TABLE 4. ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS FOR ALL THE CHARACTERS STUDIED.

Parents	Days to heading	Osmotic pressure (m osm/kg)	Stomatal frequency	Stomatal size (μm^2)	1000-grain weight (g)	Carbohydrates (%age)	Grain yield per plant (g)
Males							
1. Pak. 81	2.537	-45.926	-0.087	-17.188	-2.117	-0.567	0.046
2. K-1595	-3.796	4.241	0.019	1.236	2.181	0.466	-0.291
3. LU26S	1.259	41.685	0.069	15.952	0.064	0.101	0.246
Females							
1. High ABA 3	-2.796	16.463	-0.293	8.652	2.219	0.681	1.036
2. High ABA 4	-3.685	56.463	-0.037	1.255	2.086	0.612	-0.097
3. High ABA 6	-1.907	-72.092	-0.415	-1.408	0.819	0.187	-0.866
4. Low ABA 3	1.315	17.908	0.285	-2.466	-0.647	-0.172	1.466
5. Low ABA 4	3.426	-33.648	-0.237	-1.614	-2.047	-0.636	-1.440
6. Low ABA 6	3.648	14.908	0.696	-4.418	-2.430	-0.672	-0.099

TABLE 5. ESTIMATES OF SPECIFIC COMBINING ABILITY FOR ALL THE CHARACTERS STUDIED.

Crosses	Days to heading	Osmotic pressure (m osm/kg)	Stomatal frequency	Stomatal size (μm^2)	1000-grain weight (g)	Carbohydrates (%age)	Grain yield per plant (g)
High ABA 3 x Pak. 81	0.241	-19.962	0.109	24.169	0.806	0.329	-3.372
High ABA 3 x K-1595	0.907	-58.796	-0.230	11.709	-0.625	-0.175	1.791
High ABA 3 x LU26S	-1.148	78.760	0.120	-35.878	-0.181	-0.155	1.581
High ABA 4 x Pak. 81	-1.870	-0.962	-0.313	9.116	-1.594	-0.395	2.053
High ABA 4 x K-1595	1.463	16.537	0.381	7.656	2.442	0.658	-0.343
High ABA 4 x LU26S	0.407	-15.573	-0.069	-16.771	-0.847	-0.263	-1.710
High ABA 6 x Pak. 81	-1.315	47.593	0.731	-17.214	1.406	-0.092	1.116
High ABA 6 x K-1595	2.019	-11.241	-0.707	-28.211	-1.625	0.017	-0.008
High ABA 6 x LU26S	-0.704	-36.352	-0.024	45.426	0.219	0.076	-1.108
Low ABA 3 x Pak. 81	0.796	-43.741	-0.902	38.520	-0.594	0.016	-0.359
Low ABA 3 x K-1595	-1.204	85.092	0.793	5.370	-0.992	-0.457	-1.862
Low ABA 3 x LU26S	0.407	-41.352	0.109	-43.890	1.585	0.441	2.221
Low ABA 4 x Pak. 81	1.019	-17.185	-0.046	-38.919	-0.861	-0.603	-0.240
Low ABA 4 x K-1595	-1.648	-32.018	0.648	17.251	0.575	0.420	-1.277
Low ABA 4 x LU26S	0.630	49.204	-0.602	21.668	0.286	0.183	1.517
Low ABA 6 x Pak. 81	1.130	34.259	0.420	-15.671	0.839	0.746	0.802
Low ABA 6 x K-1595	-1.537	0.426	-0.885	-13.671	0.225	-0.464	1.699
Low ABA 6 x LU26S	0.407	-34.685	0.465	29.446	-1.063	-0.282	-2.501

LABA 4 x LU26S and HABA 6 x Pak. 81. SCA effects were positive in 50% of the crosses for stomatal frequency with highest SCA effects being scored by LABA 3 x K-1595, followed by LABA 6 x Pak. 81, LABA 4 x K-1595 and LABA 4 x LU26S hybrids (Table 5).

For stomatal size, highest negative SCA effects were exhibited by hybrid LABA 3 x LU26S, followed by LABA 4 x Pak. 81 and HABA 3 x LU26S hybrids. Nine of the 18 crosses depicted positive SCA effects for 1000-grain weight. Hybrid HABA 4 x K-1595 was found to be the best specific combiner. Other crosses showing good SCA effects included LABA 3 x LU26S, HABA 6 x Pak. 81, LABA 6 x Pak. 81 and HABA 3 x Pak. 81 hybrids.

The SCA effects were not much variable among crosses for grain yield, ranging from -3.372 (HABA 3 x Pak. 81) to 2.221 (LABA 3 x LU26S). Highest SCA effect were exhibited by cross LABA 3 x LU26S. Positive SCA effects were displayed in 8 of the 18 crosses. Such positive effects were reasonably impressive in some other crosses *viz.,* HABA 3 x K-1595, LABA 6 x HABA 3 x LU26S and LABA 4 x LU26S.

Amongst the crosses displaying positive SCA effects for grain yield and other plant traits, majority of them involved poor x good general combiner parents, which indicate that heterosis observed in these crosses was mostly because of non-additive effects. Therefore, selection in the subsequent generation has to be delayed till later generations. Only two crosses *viz.,* LABA 3 x LU26S and HABA 3 x LU26S involved parents with positive GCA effects for grain yield, indicating that selection will be more reliable in early generations due to involvement of additive gene effects.

References

1. K. Dorffling, J. Streich, W. Kruse and B. Maxfeldt, Z. Pflanzenphysiol, **81**, 43-56, L.G. Palleg and D. Aspinall, *The Physiology and Biochemistry of Drought Resistance in Plants* (Academic Press, New York).
2. L.G. Palleg and D. Aspinall, *The Physiology and Biochemistry of Drought Resistance in Plants* (Academic Press, New York), pp. 330-31.
3. Parkas and P. Rajathy, Proc. Madrid. Symp. UNESCO, Paris (1955).
4. A.M. Migahid, Proc. Madrid. Symp., UNESCO, Paris (1961).
5. P.V. Singh, M.B. Singh, Z. Ahmad and A.N. Khan, Ind. J. Farm Sci., **1**, 21 (1973).
6. A.R. Chowdhry, N.A. Chowdhry and B. Ahmad, Pak. J. Agric. Sci., **17**, 5 (1980).
7. V.I. Nakhaeva and N.A. Kalashnik, Sibirskii Vestnik Sel' skokhozyaistvennoi Nauki, **2**, 37 (1985), Pl. Br. Abstr, **57**(8) 6734(1987).
8. A.S. Redhu, R.K. Singh and O.P. Luthra, Haryana Agric. Univ. J. Res., **16**, 228 (1986).
9. M.S. Sadiq, A. Shakoor and M. Yousaf, Pak. J. Agric. Sci., **14**, 53 (1977).
10. V.P. Shamamin, S.I. Leont'ev and S.L. Petukhovskii, In Reservy Uvelicheniya Proizvodstva Zernal Zapadnoi Sibiri, Omsk, USSR (1985).
11. R.P. Singh, R.B. Singh and S. Singh, Ind. J. Gen. Pl. Br., **45,** 569 (1985).
12. R.G.D. Steel and J.H. Torrie, *Principals and Procedures of Statistics* (McGraw Hill Book Company, New York, 1980).
13. D. Kempthrone, *An Introduction to Genetics Statistics* (John Wiley and Sons, Inc., New York, 1957).