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Tolerance to drought stress among selected Indian wheat cultivars

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SUMMARY

Experiments were designed to examine differences in some morpho-physiological characters among wheat genotypes in response to drought stress at anthesis and maturity and to determine the relationships between these characters. In three sets of experiments, one set was evaluated under well-irrigated conditions and two sets under drought stress conditions by developing terminal drought stress at anthesis in one set and at maturity in the other, for 2 years. Genotypes differed in their response at both stages of plant growth for grain yield, days to heading, excised-leaf water loss, leaf membrane stability and relative water content under drought stress. Under irrigated conditions differences in the genotypes for water retention traits were not clear. There were significant genotype × environment interactions. Terminal drought stress resulted in reduced mean values and variability for all characters. The varieties WH 147 and WH 147(U) showed a combination of drought resistance, water retention and high grain yield, whereas C 306, Kharchia 65 and Hindi 62 showed a lower percentage injury in plasma membrane and better water retention in the leaves. Drought resistance index was associated with other characters.

INTRODUCTION

Wheat is mainly grown in rainfed areas of the world. In developing countries, 37% of the area is semi-arid in which available moisture is the primary constraint to wheat production. In India, about 30% of the area in wheat remains unirrigated every year (Anon. 2000). Climatic variability in these marginal environments causes large annual fluctuations in yield. Selecting wheat genotypes with better adaptation to water stress should increase the productivity of rainfed wheat (Rajaram 2001).

Genetic improvement of crops for drought resistance requires a search for possible physiological components of drought resistance and the exploration of their genetic variation. Breeding for improved drought resistance has emerged through four basic approaches (Turner 1986). The first approach was to breed for high yield and to assume that this will provide a yield advantage under suboptimal conditions, though this is often not the case (Rajaram 2001). The second approach was to breed for maximum yield in the target environment. This approach suffers from the problems that water-limited environments are notably variable from year to year and that the expression of variability for yield and its components in this environment is also low (Ludlow & Muchow 1990). The third approach involves the development of cultivars for water-limited environments through selection and incorporation of physiological and morphological mechanisms for drought resistance through traditional breeding programmes. To this end, considerable progress for rapid screening methods has been made (Kumar & Singh 1998). The fourth approach for breeding under water-limited conditions does not utilize multiple physiological selection criteria, but aims to establish a single drought-resistant character which will benefit yield under water-limited conditions and then to incorporate it into the existing breeding programme. Consequently, there have been many suggestions that improvement in yield could be achieved by identifying physiological characteristics or traits which could be included in a set of selection criteria by plant breeders (Lacape *et al.* 1998; Alves & Setter 2000). Several strategies have been devised to overcome the problem of drought stress.

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Drought screening tests have been identified for use in breeding programmes (Dhanda *et al.* 1995; Nagarajan *et al.* 1998).

Assessment of water loss from excised leaves (ELWL) has shown promise for characterizing drought resistance in wheat genotypes (Clarke 1987; McCaig & Romogosa 1991). This trait is moderately heritable (Clarke & Townley-Smith 1986) and can be easily determined in a large population (Dhanda & Sethi 1998). Following excision, stomata close and after 20–30 min, the rate of water loss enters a linear phase that lasts for several hours (McCaig & Romagosa 1991). During this phase the water is lost from incompletely closed stomata. Sinclair & Ludlow (1986) noted that there is no conclusive proof that stomata of excised leaves are fully closed. Consequently, Clarke & Richards (1988) proposed to use the term residual transpiration, defined as the rate of water loss from excised leaves at minimum stomatal aperture, in place of cuticular transpiration. Relative water content (RWC) has also been reported as an important indicator of water stress in leaves (Merah 2001). RWC is closely related to cell volume, therefore it may more closely reflect the balance between water supply to the leaf and transpiration rate (Farquhar *et al.* 1989). This influences the ability of the plant to recover from stress and consequently affects yield and yield stability (Jones *et al.* 1989).

Breeding for improved drought-tolerant varieties is mainly achieved through the exploitation of high yield potential under irrigated and drought stress conditions (Turner 1986). Blum (1988) advocated the use of stability analysis (Eberhart & Russell 1966) to define stress resistance in terms of yield, provided that the major components of variation in the environmental index could be attributed to water deficit. Fischer & Maurer (1978) proposed a drought susceptibility index on the basis of grain yield under irrigated and drought stress conditions. This approach considers neither the confounding effects of flowering time on yield, nor the effects of yield potential on the slope of the regression. Bidinger *et al.* (1987) proposed a drought resistance index that is based on residual variation in grain yield adjusted for experimental error. This seems to be a better parameter for categorization of drought-resistant cultivars. Improvement of yield under drought stress conditions should combine a reasonably high index of drought resistance with specific plant factors which would buffer the yield against severe reduction under stress (Blum 1988). Genetic variation for yield as well as a drought resistance index is limited (Ludlow & Muchow 1990). However, it can be further exploited by identification of single or multiple morphological traits for drought resistance. The aim of the present study was to establish the extent of genetic variation and interrelations among diverse wheat genotypes for simply measurable traits for drought resistance.

MATERIALS AND METHODS

Thirty wheat genotypes differing in their performance under drought stress (Table 1) were grown in three individual experiments. In one set, drought stress during anthesis was created by withholding irrigation at 30 days after sowing. In a second set drought stress during maturity was created by withholding irrigation at 70 days after sowing. The third set was conducted under irrigated conditions and was used to collect the data at both anthesis and maturity stages of plant growth. Thus, in each year there were three experiments, one under irrigated and two under drought stress conditions. This design was repeated in each of 2 years, 1991–92 and 1992–93 under field conditions at the CCS Haryana Agricultural University, Hisar, Haryana, India at 29° 10′ N, 65° 46′ E longitude at 215 m a.s.l. The rainfall in this part of the state is very low during *rabi* season. The total rainfall during the crop season was 39·1 mm and 32·3 mm during growing seasons 1991–92 and 1992–93, respectively.

All genotypes in each environment were randomized in three blocks and sown in the first week of November during the normal *rabi* season. The plot size in both environments was a single row of 3 m length with a spacing of 30 × 10 cm. The data for grain yield per plant were recorded as the average of five competitive plants selected randomly from each row. Each year under drought stress conditions, the experiments were terminated after recording the data for various characters at anthesis and maturity stages. Out of 30 genotypes selected, about half were drought resistant and the remainder were agronomically adapted and gave higher yield under irrigated conditions. The genotypes C 306, Kharchia 65 and VL 421 are well known for their drought tolerance. WH 147, WH 147(U), WH 331, WH 533, WL 410, WL 1562 and Kundan were recently released varieties for their suitability under rainfed conditions. RL 6, RL 7, RL 68 and RL 84 are newly developed lines from Himachal Pradesh Agricultural University, Palampur, Himachal Pradesh, India, bred for drought stress conditions and having rye–wheat translocations.

At the time of recording the data in drought stress experiments soil moisture was determined gravimetrically at 0–15 cm, 15–45 cm, 45–75 cm and 75–105 cm depth spaced at a 3 m distance throughout the experiments. The average values of moisture content for both years are given in Table 2. No significant differences were observed between the various sites of soil sampling at each moisture level throughout the experiment at a particular depth. Soils of Hisar are sandy loams, therefore plant wilting commenced at 10–13 % moisture level in the upper 15 cm layer of soil at anthesis and at 9–11 % moisture at crop maturity. For recording observations for excised-leaf water loss (ELWL), relative water content (RWC) and leaf membrane stability (LMS), the plants were observed

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Table 1. *Distinguishing characters of 30 wheat genotypes evaluated*

Genotype	Pedigree	Year of release	Characteristics
WH 147	E 4870/C 303//S 339/PV 18	1979	Double dwarf, suitable for medium fertility, rainfed and timely sown conditions
WH 147(U)	E 4870/C 303//S 339/ PV 18//*Agropyron* spp.	–	Double dwarf, suitable for medium fertility, rainfed and timely sown conditions, and resistant to brown rust
Lok 1	S 308/S 331	1981	Double dwarf, early maturing, suitable for timely sown conditions, resistant to salinity/alkalinity
Lok 1(U)	S 308/S 331//*Agropyron* spp.	–	Double dwarf, early maturing, timely sown, resistant to salinity, alkality and brown rust
WH 157	NP 876/S 308// Ciano 'S'/E 8156	1980	Double dwarf, timely maturing, timely sown, resistant to salinity and alkalinity
Kharchia 65	Selection from Kharchia local EG 953	–	Tall, late maturing, suitable for saline and rainfed conditions
HW 2001	II5, 38/AN/y yt 54// N 10B/ILR 64		Double dwarf early maturing, for irrigated conditions
CPAN 1992	Bob-white 'S'/Au// Kalyansona/Bb/Wop 'S'	–	Single dwarf, suitable for irrigated and timely sown conditions
C 306	Regent 1974/Ch 23// C 591/P 19/C 281	1965	Tall, medium late maturing, for low fertility, rainfed and timely sown conditions
K 68	NP 773/K 13	1968	Tall, medium in maturity, suitable for timely sown and rainfed conditions
WH 331	WH 107/WH 120// HD 2009	1982	Single dwarf, medium late maturity, suitable for low fertility and rainfed conditions
WH 533	Buck buck/Bluejej// Gryo/EMU	1993	Single dwarf, suitable for rainfed and timely sown conditions
Hindi 62	Kenya 48 F/L 1/E 144// N 245.44-25	–	Single dwarf, timely sown, late maturing and resistant to high temperature and drought conditions
PBW 65	USA 255/K 816/WL 202	1984	Single dwarf, medium late, suitable for timely sown, low fertility and rainfed areas
WL 410	S 63/S 326/Kalyansona	1975	Double dwarf, for timely sown, low fertility and rainfed conditions
WL 1562	Mapo/Tob 'S'//1856/ Kal/Bb	1984	Single dwarf, medium late, for timely sown, low fertility and rainfed conditions
Kundan	Tanori 71/MP 890	1985	Double dwarf, medium late, for timely sown low fertility rainfed conditions
HPW (DL) 30	HI 784/DL 99-7	–	Single dwarf for late sown, irrigated conditions
VL 421	S 64/Y50G	1979	Double dwarf for timely sown, low fertility and rainfed conditions
HD 2329	HD 1962/E 4870//XX 65/ HD 1553/UP 262	1985	Double dwarf, medium maturing, for irrigated conditions
HD 2329(U)	HD 1962/E 4870//XX 65/ HD 1553/UP 262/*Agropyron* spp.	–	Double dwarf, medium maturing, suitable for irrigated conditions and resistant to brown rust
HPW 42	VEE 'S'/4/PVN 'S'//CBB/CNO 'S'/3/JAR/OR 2 'S'	1992	Double dwarf, early maturing, for timely sown, rainfed and high hill areas
HS 295	QT 24Z/1A 5 55/ACD 'S'//ALD 'S' Nath/PJN 'S' 1992 PEL 'S'	–	Double dwarf, early maturing, for timely sown rainfed conditions
HPW 56	Maris Hantsman/HD 234/HD2160	–	Double dwarf, for late sown, rainfed conditions
CPAN 3004	Gallo/Aust II-61-157// CNO 67/Veery 'S' No. 3	–	Double dwarf, for late sown, rainfed conditions
HPW 65	RL3 CPAN 1922	–	Double dwarf, for late sown and rainfed conditions
RL 6	UPT 72142/Girija	–	Single dwarf, for timely sown and rainfed conditions
RL 7	UPT 72142/Girija	–	Tall, for timely sown and rainfed conditions
RL 68	UPT 74303/Sonalika	–	Single dwarf for early sown, rainfed conditions
RL 84	UPT 72142/HS 74	–	Double dwarf for early sown, rainfed conditions

–, Year of release not reported.

Table 2. *Average gravimetric soil moisture percentage of drought stress experiment for 2 years. Values are means with* S.E. *(14* D.F.*) in parentheses*

Depth (cm)	1991–92		1992–93	
	At anthesis	At maturity	At anthesis	At maturity
0–15	11·28 (1·23)	8·94 (1·23)	12·26 (1·36)	10·34 (2·34)
15–45	16·13 (1·54)	13·37 (2·11)	17·71 (1·98)	12·87 (1·87)
45–75	21·84 (2·37)	16·06 (1·56)	21·18 (3·17)	18·46 (2·38)
75–100	24·90 (1·98)	21·31 (1·85)	23·67 (2·35)	22·13 (1·76)

for temporary wilting in the evening and only those plants which did not recover during the night were measured on the following day. The data at anthesis were collected between 60–70 days after sowing, and data at maturity were collected between 95–105 days after sowing (DAS) in the drought stress experiments. In the irrigated experiment, the data for days to heading and maturity were collected between 82–100 DAS and at maturity 125–140 DAS.

Data for ELWL and RWC were observed from the flag leaf and two fully expanded preceding leaves respectively. To avoid any complication due to variation in level of mid-day water deficit, predawn measurements for both characters were recorded. For ELWL the leaves were weighed at three stages, viz., immediately after sampling (fresh weight), then dried in an incubator at 28 °C at 50% R.H. for 6 h, and then dried again in an oven for 24 h at 70 °C as proposed by Clarke (1987). ELWL was calculated from the following formula:

$$\text{ELWL} = [(\text{Fresh weight} - \text{Weight after 6 h})/(\text{Fresh weight} - \text{Dry weight})] \times 100$$

The samples for RWC were also weighed immediately as fresh weight (FW), then sliced into 2 cm sections and floated on distilled water and weighed to obtain turgid weight (TW). The leaf discs were dried in the oven at 60 °C for 24 h and then dry weight (DW) obtained. The RWC was calculated using the formula of Barrs (1968):

$$\text{RWC (\%)} = [(\text{FW} - \text{DW})/(\text{TW} - \text{DW})] \times 100.$$

About 20 leaf sections of 2 cm length were taken from the flag and penultimate leaves from drought stressed and irrigated plants. These samples were washed rapidly three times with deionized water; 20 ml deionized water was then added, they were warmed to 45 °C for 1 h, shaken well and the electrical conductivity was measured (Blum 1988). The leaf tissues were then killed by autoclaving all the samples for desiccation (T) and control (C) treatments. Leaf membrane stability of leaf tissues was calculated as percentage of injury using the equation:

$$\text{Injury (\%)} = [1 - \{(1 - T_1/T_2)/(1 - C_1/C_2\}] \times 100$$

where, T_1 and T_2 are the first and second conductivity measurements for the desiccation treatment, respectively. C_1 and C_2 are the first and second measurement of the control, respectively.

Drought resistance for an individual genotype was computed using the formula given by Bidinger *et al.* (1987) as $\text{DRI} = (Y_a - Y_{est})/\text{SES}$, where Y_{est} and Y_a are the yield estimated by regression and actual yield under stress for the cultivars, respectively, and SES is the standard error of the multiple regression (Bidinger *et al.* 1987). This method is also capable of removing the effect of the intervening variable for effect of days to heading on the grain yield through regression and provides an unbiased estimate of index of resistance (Arraudeau 1989). Positive values of DRI denote drought tolerance.

RESULTS

Analyses of variance

Analyses of variance for each experiment (one irrigated experiment and two drought stress experiments) were carried out separately over the years (Table 3). Under irrigated conditions, the genotypes differed significantly for all the characters except ELWL. Variation due to years and the genotype × year interaction was also significant indicating that these characters were more variable over the years. Under drought stress conditions, one experiment was subjected to drought stress at 30 DAS and the data for ELWL, RWC and LMS were recorded at anthesis before permanent wilting of plants. In the second experiment, the drought stress was created at 70 DAS and data for days to heading and grain yield/plant were recorded at maturity. The differences in the years and genotypes were more pronounced under drought stress than under irrigated conditions for ELWL and RWC. This could provide scope for selecting these genotypes for their performance under drought stress

Table 3. *Mean squares of 30 genotypes of wheat for different characters under irrigated (Irr) and drought stress (Dr) for 2 years*

Source of variation	D.F.	Excised-leaf water loss (%)		Relative water content (%)		LMS (Injury %)	Grain yield/ plant (g)		Days to heading	
		Irr	Dr	Irr	Dr	Dr	Irr	Dr	Irr	Dr
Year (Y)	1	28·2	169·2	165·8	714·2	25·8	136·7	50·5	136·1	87·5
Rep./Year	4	95·6	114·7	77·7	38·2	26·1	29·68	27·6	42·5	66·3
Genotype (G)	29	62·8	156·3	98·4	204·1	156·3	113·8	96·5	126·7	68·3
G×Y	29	57·9	39·1	46·6	52·5	16·9	56·3	28·4	91·3	76·1
Pooled error	116	48·3	35·1	51·8	29·7	11·7	14·2	1·3	26·7	19·9

conditions. Interaction due to genotype into year was also significant for RWC, grain yield per plant and days to heading under drought stress environment, but there was no similar effect for ELWL and LMS. This may be due to uniformity in the expression of variability over the years for these characters.

Mean performance

Comparative mean performance of genotypes for water retention parameters (ELWL and RWC) indicated that the genotypes WH 147(U), Kharchia 65, C 306, WL 1562, VL 421 and HPW 42 were significantly better than the overall mean for minimum water loss and maximum water retention (Table 4). In addition, WH 147, Lok 1(U), WH 157, WH 533, Hindi 62, HPW 65, RL 6 and RL 68 were better than the overall mean for either minimum water loss, or maximum water retention. The majority of these genotypes also showed significantly lower injury in their plasma membranes by reducing ion leakage under drought stress. In addition, WH 331, RL 7 and RL 84 had greater leaf membrane stability.

Average grain yield per plant under irrigated conditions ($14·7 \pm 0·89$ g) was significantly higher than that in drought stress conditions ($3·7 \pm 0·45$ g). The varieties WH 147(U), HD 2329(U) and RL 6 showed significantly higher yields under both irrigation and drought stress. The varieties CPAN 1992, K 68 and HD 2329 were higher yielding under irrigated conditions, while WH 147, Kharchia 65, C 306 and RL 6 were higher yielding under drought stress. Significantly higher DRI for WH 147, WH 147(U), Kharchia 65 and C 306 suggested that the high yields of these varieties under drought stress may be partly due to their resistance potential. The high yields in HD 2329(U) and RL 6 under drought stress may be either due to their high yield potential under irrigated conditions and/or earliness. In the present case, the DRI was calculated by using resistance potential as the response variable, and yield potential and escape mechanism as the independent variables in a multiple regression approach. Therefore, significantly higher values of DRI for these varieties were indicative of their resistance potential rather than of yield potential and escape. Thus, the overall mean performance indicated that C 306 was the variety most tolerant to drought stress followed by Kharchia 65, WH 147(U) and WH 147, as these varieties showed the highest score of DRI as well as better performance in drought-related traits.

Correlations

The genotypes having lower ELWL exhibited greater membrane stability ($r = 0·40$), higher grain yield ($r = -0·36$; D.F. $= 28$; $P \leqslant 0·05$) and higher indices of DRI ($r = -0·45$; D.F. $= 28$; $P \leqslant 0·05$) (Table 5). The varieties showing high water content under drought stress conditions exhibited less injury ($r = -0·60$; D.F. $= 28$; $P \leqslant 0·05$), higher grain yield ($r = 0·69$; D.F. $= 28$; $P \leqslant 0·05$) and higher DRI ($r = 0·76$; D.F. $= 28$; $P \leqslant 0·05$). Leaf membrane stability and grain yield/plant were also significantly associated with all other characters except for DRI and days to heading under irrigated conditions. A significant negative correlation of grain yield per plant with days to heading ($r = -0·44$; D.F. $= 28$; $P \leqslant 0·05$) under drought stress conditions suggested that the varieties earlier in flowering were better in yield under drought stress conditions. DRI appeared to be the most important variable because the genotypes having higher values of DRI also had better water retention, lesser injury in plasma membrane and higher grain yield under drought stress conditions.

DISCUSSION

Variation due to genotypes was significant for all characters. This suggested that the magnitude of differences in genotypes was sufficient to provide some

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Table 4. *Mean performance of 30 wheat genotypes over the years/environments for various characters at seedling and maturity stages of plant growth under irrigated (Irr) and drought stress (Dr) conditions for 2 years*

Genotype	Excised-leaf water loss (%)	Relative water content (%)	LMS† (Injury %)	Grain yield/ plant (g)		DRI (indices)	Days to heading	
	Dr	Dr	Dr	Irr	Dr	Irr and Dr	Irr	Dr
WH 147	71·6	68·0	23·5	17·0	6·3	1·7	82·0	75·0
WH 147(U)	68·1	66·0	20·6	18·3	6·8	2·0	84·3	74·0
Lok 1	68·9	56·7	42·5	15·8	4·2	0·3	91·7	84·1
Lok 1(U)	72·3	65·0	26·0	12·3	4·6	0·9	85·0	79·1
WH 157	77·9	64·1	40·4	16·3	4·3	0·5	95·1	87·0
Kharchia 65	62·3	63·9	19·9	11·4	5·5	2·0	100·0	89·0
HW 2001	81·1	42·2	62·2	16·5	1·6	−1·8	92·9	84·3
CPAN 1992	82·2	45·1	53·9	18·6	3·7	−0·7	100·3	80·0
C 306	63·3	75·9	20·5	12·6	7·9	3·9	104·7	89·0
K 68	81·3	41·0	55·2	18·7	1·0	−2·1	117·7	92·1
WH 331	73·0	41·9	31·3	11·2	2·1	−0·1	106·7	84·9
WH 533	67·9	57·3	62·3	16·8	2·6	−1·4	109·3	83·0
Hindi 62	64·0	43·9	35·6	13·9	3·4	0·2	116·3	93·0
PBW 65	80·1	53·1	49·3	12·5	3·6	−0·6	99·3	83·1
WL 410	78·0	43·1	56·0	14·6	3·9	−0·9	105·0	83·3
WL 1562	63·9	58·1	32·2	16·7	4·4	0·1	111·1	82·8
Kundan	80·1	56·9	48·0	10·9	3·0	0·2	116·4	84·7
HPW (DL) 30	79·1	62·1	60·0	14·1	3·7	0·1	102·1	83·0
VL 421	67·9	59·8	32·0	9·6	3·2	0·7	106·0	88·3
HD 2329	68·9	41·9	71·0	18·1	4·0	−0·8	89·9	76·0
HD 2329(U)	79·2	43·1	65·0	20·1	4·8	−0·2	90·0	75·7
HPW 42	67·0	57·9	49·0	14·4	4·6	−0·5	86·1	74·3
HS 295	81·0	35·3	41·0	14·5	2·5	−1·1	111·7	82·3
HPW 56	80·0	55·7	56·0	9·4	3·1	0·4	109·7	84·3
CPAN 3004	83·1	42·7	57·0	17·3	1·9	−1·0	107·3	85·7
HPW 65	65·0	55·7	33·0	14·5	1·6	−1·2	114·3	87·7
RL 6	67·2	52·9	42·0	17·7	5·1	−0·2	116·7	81·7
RL 7	65·9	47·9	36·0	10·2	2·6	0·1	125·0	85·7
RL 68	61·0	36·0	76·0	14·2	2·3	−1·0	125·0	84·0
RL 84	71·1	40·0	38·0	12·4	3·0	−0·1	110·3	83·0
Mean	72·9	51·9	44·4	14·7	3·7	0·0	103·8	83·2
S.E. (m)a No. (29 D.F.)	2·42	2·94	2·22	1·40	0·47	0·62	2·11	1·82
S.E. (m)b No. (59 D.F.)	–	–	–	0·89	0·45	–	4·40	1·90

S.E. (m)a: for comparison of mean values of two entries in the same column; S.E. (m)b: for comparison of overall means of different columns, $P<0·05$ and $P<0·01$.

† LMS (Injury %) indicate membrane stability in terms of percentage of injury in plasma membrane, i.e., lesser the injury more the stability of the membrane.

scope for selecting traits for improvement in drought tolerance of wheat genotypes. The reduction in variability under stress environments particularly for grain yield and days to heading may be due to either limited expression of genotypes and/or high environmental variations (Table 3) (Blum 1988; Ludlow & Muchow 1990). The genotypes WH 147(U), Kharchia 65, C 306, WL 1562, VL 421 and HPW 42 showed significantly less water loss and better water retention under drought stress conditions (Table 4). This suggested that these varieties were capable of tolerating drought stress through maintaining the water balance in their leaves. Assessment of water loss from excised leaves has shown promise for characterizing drought resistance of wheat genotypes (McCaig & Romagosa 1991; Dhanda *et al.* 1998) and is moderately heritable (Clarke & Townley-Smith 1986). The genotypes with a lower water loss also gave higher grain yield ($r=-0·36$) and higher DRI ($r=-0·45$). This trait is more useful for selecting genotypes at the earlier rather than later stages of plant growth. This may be due to succulency in plants which may disappear at later

Table 5. *Correlation coefficients for various drought-related characters among 30 wheat genotypes under irrigated and drought-stress conditions for 2 years*

Character	Environment	Relative water content (%)	Leaf membrane stability (%)	Grain yield/plant (g)	Days to heading	DRI
Excised-leaf water loss	Droughted	−0·33	0·40*	−0·36*	−0·05	−0·45*
Relative water content	Droughted		−0·60**	0·69**	−0·08	0·76**
Leaf membrane stability	Droughted			−0·49**	−0·14	0·73**
Grain yield/plant	Irrigated				−0·31	−0·31
	Droughted				−0·44*	0·81**
Days to heading	Irrigated					0·3
	Droughted					−0·03

DRI, drought resistance for an individual genotype.
* $P<0.05$; ** $P<0.01$.

stages and the expression may further be decreased due to leaf scorching (Clarke 1987).

Genotypes showing least injury to their plasma membrane under drought stress were Kharchia 65 followed by C 306, WH 147(U) and WH 147. Among these, C 306 and Kharchia 65 are known for their stress tolerance (Bansal & Sinha 1991; de Leon *et al.* 1995). The use of these varieties for improvement of stress resistance in existing wheat varieties may increase the yield of wheat under rainfed conditions. Leaf membrane stability also appeared to be a reliable character under drought stress as it was related to a majority of the drought-related traits, such as relative water content, grain yield and DRI. The degree of membrane stability under stress, evaluated by ion leakage, correlated well with other plant processes (Blum 1988). Disintegration of the plasma membrane occurs primarily due to heat stress as a secondary response to drought stress (Hale & Orcut 1987). Evaluation of cell membrane stability involves the measurement of the rate of solute leakage from leaf tissues after exposure to drought and may be used as an efficient method of detecting heat and drought tolerance in crop plants (Blum 1988). Thus C 306, Kharchia 65 and WH 147(U) combined better water retention and little injury to the plasma membrane.

WH 147(U) showed a combination of higher yield under both conditions. This variety is an improved strain of WH 147 which had a combination of high yield potential with drought-related traits and early days to heading which can buffer grain yield against severe yield reductions under drought stress (e.g. Blum 1988). Inconsistent performance of the majority of the genotypes under irrigated and drought stress environments (e.g. C 306 and Kharchia 65) indicated that the traits which contributed to high yield under irrigated conditions may be different from those of high yield under drought stress (Ceccarelli 1987). This indicated that the grain yield in these varieties may be due to the contribution of drought-tolerant traits rather than the yield potential. In an attempt to separate the effect of yield potential from drought susceptibility, Fischer & Maurer (1978) proposed a susceptibility index (*S*). This index, however, did not consider time to flowering associated with drought escape, and a correction has to be made for differences in anthesis date. Yield under drought is often negatively related with anthesis date (Bidinger *et al.* 1987). Furthermore, this index was also positively related with yield potential (Ceccarelli 1987) and therefore may not be a true indicator of drought resistance. Bidinger *et al.* (1987) proposed a drought response index (DRI) based on residual variation in grain yield. This was positively associated with yield under drought and independent of yield potential and time to flowering and can be considered as a good criterion for assessment of drought-resistant traits which would be manipulated as independent genetic characters. DRI values indicated that the variety C 306 was the most tolerant followed by Kharchia 65. These varieties also performed better for other drought-related traits except for earliness indicating their tolerance to and/or avoidance of drought stress (Bansal & Sinha 1991; Dhanda & Sethi 1996). High values of DRI for WH 147(U) and WH 147 were not due to their escape from severe drought but due to the contribution of drought-related traits, because the effect of earliness has been removed in calculating DRI (Bidinger *et al.* 1987).

The simple correlation of grain yield for plants with the characters excised-leaf water loss, relative water content, leaf membrane stability, day to heading and drought resistance index indicated that selection for grain yield under drought-stress conditions may provide desirable results. As yield is influenced by several variables, it cannot be used as a selection criterion. Therefore, improvement of the yield under drought stress should combine a reasonably high yield potential with a specific plant factor which would buffer yield against a severe reduction under stress (Jones *et al*. 1989). The use of C 306, Kharchia 65, WH 147(U) and WH 147 in a breeding programme may provide desirable segregants for drought resistance. DRI was the most reliable indicator of drought resistance in this set of material, in terms of number and magnitude of correlation coefficients followed by measurements of membrane stability and relative water content.

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