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Membrane Thermal Stability at Different Developmental Stages of Spring Wheat Genotypes and Their Diallel Cross Populations

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Abstract: Membrane thermal stability (MTS) can be a significant selection criterion for heat stress tolerance. MTS is determined by measuring of electirical conductivity of aquause phase in which leaf tissue exposure to high temperature. This research was conducted to investigate the membrane stability assay measured by two different methods, namely MTS and relative injury (RI). The second objective of this experiment was to determine the effects of different growth stages of four spring wheat parents and their six half F_2 diallel cross progenies grown in the field on membrane stability. Measurements were taken at different growth stages (seedling, stem elongation and early milk). The MTS and RI assays gave similar results at the three different growth stages. However, growth stages significantly affected the MTS and RI values of genotypes. Membrane stability parameters of genotypes decreased during the later developmental stages. Specific combining ability effects were superior to general combining ability effect for all measurements, indicating that membrane thermal stability was mediated mainly by non-additive gene actions. Membrane stability of flag leaf at the early milk stage was significantly correlated with grain yield. The parent of Genç 99 and 84ÇZT04 had low yield potential, whereas Chil's and Seri 82 had high yield potential. Grain yield, spike yield and kernel weight of F_2 population were found higher than their parents. These results suggest that genetic variation among genotypes for membrane stability can be utilized in wheat breeding in heat-stressed environments.

Key Words: Diallel, membrane thermal stability, wheat, grain yield

Yazlık Buğday Genotipleri ve Diallel Melez Populasyonlarının Farklı Gelişme Dönemlerinde Yüksek Sıcaklık Membran Kararlılığı

Öz: Yüksek sıcaklığa toleransta hücre zarlarının kararlılığı önemli bir fizyolojik seleksiyon kriteri olabilir. Yüksek sıcaklık membran kararlılığı, yüksek sıcaklığa maruz bırakılan yaprak dokusunun içerisinde bulunduğu sulu ortamdaki elektriksel iletkenliğin ölçümüyle belirlenmektedir. Bu araştırma, tarla koşullarında yetiştirilen 4 yazlık buğday anacı ve bunların altı F_2 diallel melez döllerinde, iki farklı yöntemle (MTS, yüksek sıcaklık membran kararlılığı ve RI, zarar indeksi) hesaplanan membran kararlılığının farklı gelişme dönemlerindeki değişimlerini belirlemek amacıyla gerçekleştirilmiştir. Ölçümler, yaprak büyümesi (erken vejetatif dönem), sapa kalkma ve erken süt olum evrelerinde gerçekleştirilmiştir. MTS ve RI ölçümleri üç farklı büyüme evresinde benzer eğilim göstermiştir. Bununla birlikte, büyüme evreleri genotiplerin MTS ve RI değerlerini önemli düzeyde etkilemiştir. Genotiplerin membran kararlılığı parametreleri büyüme evresi ilerledikçe azalmıştır. Tüm ölçümlerde özel uyum yeteneğinin genel uyum yeteneğine üstünlük sağlaması, memran kararlılığı özelliklerinin yönetiminde eklemeli olmayan gen etkilerinin etkin olduğunu göstermektedir. Erken süt olum evresinde bayrak yaprak membran kararlılığı, tane verimiyle önemli düzeyde ilişkili bulunmuştur. Anaçlardan Genç 99 ve 84ÇZT04 düşük verim, Chil's ve Seri 82 yüksek verim potansiyeli göstermişlerdir. F_2 döllerinde tane verimi, başak verimi ve tane ağırlığı anaçlardan yüksek bulunmuştur. Bu sonuçlar, membran kararlılığı ölçümleri yönünden genotiplerdeki mevcut çeşitliliğin sıcak stresli çevrelerde buğday ıslahında kullanılabileceğini göstermektedir.

Anahtar Kelimeler: Diallel, yüksek sıcaklık membran kararlılığı, buğday, tane verimi

Introduction

Although wheat production in much warmer areas is technologically feasible, heat stress is a common constraint especially during anthesis and grain filling stages in many temperate environments in South and West Asia, North Africa, Australia, and the Central and Southern Great Plains of the USA (Reynolds et al. 1994a). Wheat producers are seeking new heat tolerant germplasm suited to these stressed

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areas. Chronic heat stress has been underlined as an average daily temperature of greater than 17.5°C in the coolest month of the crop growth cycle (Fischer and Byerlee 1991). High temperatures during grain growth is a main environmental factor that reduces the grain yield (Fischer 1983) because of the induction of early senescence and acceleration of grain filling activities in wheat (Paulsen 1994) due to shortening of grain filling duration and constriction of carbon assimilation (Stone 2001). Grain weight is negatively affected by high temperatures, especially those above 34°C, that reduce the duration of grain filling owing to the limited photosynthesis (Al Khatip and Paulsen 1984), and inhibit starch biosynthesis in the endosperm (Jenner 1994, Keeling et al. 1993). Stone and Nicolas (1994) have reported that losses in kernel weight (23%) occurred when the temperature was increased from 20/15 °C (day/night) to 40/15 °C on the third day after anthesis.

When heat stress is intensified during grain filling, assimilates are more likely to be yield limiting under stress than in temperate environments. Evidence for this comes from the observation that under stress, total above-ground biomass will typically show a strong association with yield (Reynolds et al. 1994b). Physiological and biochemical screening techniques as a complement to empirical breeding methods could increase selection efficiency. Plant physiological processes differ in their response to heat stress from one phenological stage to another (Fischer 1985). The genes securing heat tolerance may be lost in the breeding programs which rely mainly on only empirical selection (Reynolds et al. 1994a).

Membrane thermal stability, a measure of electrolyte diffusion resulting from heat-induced cell membrane leakage, has been used to screen and evaluate different wheat genotypes for thermal tolerance (Blum and Ebercon 1981, Saadalla et al. 1990a). This method measures the increased electrolyte diffusion resulting from heat induced cell membrane permeability. Electrical conductivity has been used as an index of membrane stability to identify heat-tolerant genotypes in wheat (Blum and Ebercon 1981) and for screening of heat-tolerant genotypes in different crops (Blum 1988). When tissues are subjected to high temperature, electrical conductivity increases due to damage to the cell membrane and consequent solute leakage.

Fokar et al. (1998) reported that there was a strong positive association across cultivars between grain weight per ear and cell membrane stability as a measure of heat tolerance, however, membrane stability may be only a small part of the numerous properties and processes that interact to provide tolerance to stress during maturation (Assad and Paulsen 2002). Another expression of membrane stability is leaf membrane stability (LMS). The genotypes having high cell viability had also high LMS and high grain yield under heat stress and LMS was significantly positively associated with heat response index (Dhanda and Munjal 2006). High temperatures at seedling growth decreased MTS in wheat (Efeoglu and Terzioglu 2007). The MTS assay is also associated with genetic variability under drought while physiological traits such as photosynthesis, stomatal conductance and canopy temperature depression are related mainly with heat tolerance (Blum 1988). It was reported differences for membrane permeability within bread and durum wheat species concerning the capability to cope with high temperatures at the stage of grain filling (Dias et al. 2009).

Saadalla et al. (1990b) estimated genetic effects for MTS by examining 90 F_5 genotypes derived from crosses among heat-tolerant and heat-sensitive wheat parents. They observed transgressive segregation in F_5 progeny means of relative injury values determined by MTS tests, suggesting that the parents had different genes contributing to heat tolerance and that the trait is not simply inherited. Both additive and dominant types of gene action were reported at the genetic direction of MTS (Dhanda and Munjal 2006).

The objectives of this study were to assess the genetic variation among genotypes for MTS and RI and their relations with yield and agronomic traits of spring wheat at different growth stages.

Materials and Methods

Cultural practices and environmental conditions: Four springs wheat cultivars were used to obtain a 4 × 4 diallel crosses excluding reciprocals. The F_1 hybrids were obtained in 2001. After a reproduction in 2002, a field experiment was established in 2002-2003 growing season to evaluate the four parents and their six F_2 progenies. The parental lines of ‘Chil's’, ‘Genç 99,’ and ‘Seri 82,’ are representative of CIMMYT germplazm. ‘Genç 99’ and ‘Seri 82’ were selected from the CIMMYT bulk ‘Ka's/Nac’ while ‘Seri 82’ was identified at CIMMYT/IWIS catalog and then released and registered as Turkish spring wheat cultivars. ‘84ÇZT04’(1976 EBMN 1852 x Y_{50} Ekal^3 x Cut.75) is a line of Cukurova University.

The trial soil was clay loam (55% clay, 33% sand, and 12% silt) and contained 16% carbonate, 1.7% organic matter, 7.9 mg P kg^{-1}, with a pH 7.9. Soil had 116 kg ha^{-1}mineral N in the upper 90 cm profile at sowing time. Total precipitation (468mm) during growing stages was below the long term average (560mm). Mean temperatures were 17.1℃ and 22.4 ℃ during the pre- and post- anthesis period, respectively. Experiment received 80 kg ha^{-1} P_2O_5 and 160 kg ha^{-1} N in three different applications of 80 kg N, 40 kg N, and 40 kg N at sowing, tillering and at the beginning of stem elongation, respectively. Each plot consisted of eight rows which were 5 m-long that were spaced 0.15 m apart and was sown at a density of 350 grains m^{-2}. Fungicide and insecticide treatments were applied to control diseases and pests, also to separate the confounding effects excepting heat stress.

Agronomic Traits: Grain yield (kg ha^{-1}) was measured in harvested plots. Test weight, measured in a sample of one kg per plot, is expressed as kg hl^{-1}. Mean kernel weight was calculated from the weight of 400 kernels plot^{-1}. Spike yield and the number of kernels per spike were determined on 40 randomly selected spikes in each plot before harvest. Stay green duration was calculated in day units as the period between sowing and physiological maturity (% 95 green color losing of plants).

Membrane Thermal Stability: Fourth, seventh and flag leaves of parent and F_2 progenies grown in the field were analyzed for MTS using the fourth leaf at the seedling growth (GS14), the seventh leaf at the stem elongation (GS32) and the flag leaf at the early milk ripe stage (GS71) and GS defines Zadoks Growth Scale (Zadoks et al. 1974). Eight fully expanded leaves of each genotype were cut from randomly selected plants for each replication. Each leave was divided into two parts to use as control and as heat-treatment. Halved leaves were placed into two different test tubes containing 10 ml de-ionized water and were held for 18 h in a refrigerator at 10°C. Thereafter, leaves were thoroughly washed with de ionized water and 15 ml de-ionized water was added. Then, one half each of the test tubes was kept at 25°C and the other half at 45°C for 1h in water bath.

Both control and heat treated samples were kept for 18 h in a refrigerator at 10°C to stabilize the content of the liquid compound after treatment period. Conductivity readings were taken at 25°C using an electrical conductivity meter for control (C_1) and heat treated (T_1) tubes. The samples were then boiled for 1 h. A second conductivity reading of the aqueous phase (T_2 and C_2) was taken at 25°C after the samples were cooled. Leaf membrane thermal stability was estimated using two different equations (Blum and Ebercon 1981):

I. Membrane Thermal Stability, MTS (%): $[1-(T_1/T_2)]$ x100

II. Relative Injury, RI (%): $100-\{[1-(T_1/T_2)]/[1-(C_1/C_2)]$ x100$\}$

Where C and T refer to electrical conductivity of control and heat treated samples, and the subscript 1 and 2 refer to electric conductivity readings before and after boiling, respectively.

Statistical Analyses: The diallel analyses of MTS and RI values were conducted according to Griffing (1956) method 2 (including parents but no reciprocals) using SAS (1998) program of Zhang and Kang (1997). Values of other agronomic traits were analyzed as a randomized block design with three replicates. Genotypes (parent and their F_2 progenies) means over all dates were compared by the least significant difference (LSD) method at P = 0.05 by SAS (1998) program. Correlations between two traits were also evaluated by SAS (1998) program.

Results

Values of grain yield and investigated agronomic traits of the four parents and their six F_2 populations are presented in Table 1. Genç 99 and 84ÇZT04 had low yield potential. Chil's was characterized as a good combiner in terms of yield and other investigated traits and its agronomic traits were generally higher than the remaining parents. Grain yield, spike yield and kernel weight of the F_2 populations were higher than their parents. The F_2 populations of Genç-99 x Chil's and 84ÇZT-04 x Chil's had the highest grain yield. Chil's and F_2 population of Genç-99 x Chil's had high stay green values.

Analysis of variance showed significant differences among genotypes for membrane thermal stability (MTS) and relative injury (RI) at all growing stages (Table 2). Mean squares for general combining ability (GCA) effects were significant only at the GS14 stage using both methods. Specific combining ability (SCA) effects were significant for both methods and across the three stages. The significant GCA and SCA variance indicate that both additive and non-additive gene actions are involved at the GS14 stage in the genotypes studied. The significant SCA effects showed that membrane stability at the GS32 and GS71 stages were mainly mediated by dominance effects.

Table 1. Yield and agronomic parameters of wheat parents and their F_2 progenies

Parents	Grain yield ($kg\ ha^{-1}$)	Test weight ($kg\ hl^{-1}$)	Spike yield (g)	Spike kernel number	Kernel weight (g)	Stay green (day)
(1) Genç 99	5053	75.3	1.75	47.4	37.0	169.3
(2) 84ÇZT04	5417	77.7	1.39	39.2	35.8	166.3
(3) Chil's	5610	76.9	2.08	52.7	39.8	173.0
(4) Seri 82	5687	71.2	1.71	47.9	35.5	168.3
Mean	5442	75.3	1.73	46.8	37.0	169.2
F_2 Populations						
1 x 2	6300	77.6	1.96	44.4	44.2	167.0
1 x 3	6340	76.2	1.94	43.2	44.9	170.3
1 x 4	6333	75.3	1.75	46.9	37.2	170.3
2 x 3	6510	76.3	1.61	39.4	40.7	169.7
2 x 4	6297	76.5	1.88	43.5	43.0	169.7
3 x 4	5363	76.1	1.80	46.0	39.2	167.7
Mean	6191	76.3	1.82	43.9	41.5	169.1
General mean	5891	75.9	1.79	45.1	39.7	169.2
$LSD_{(0.05)}$	1087	3.27	0.39	8.6	5.85	2.65
CV (%)	10.8	2.51	12.6	11.1	8.59	0.91

Table 2. Analysis of variance for membrane thermal stability (MTS) and relative injury (RI) of parents and their 4 x 4 half diallel crosses of wheat at different growing stages

		Mean Squares					
		MTS			RI		
Source of variation	Df	GS14	GS32	GS71	GS14	GS32	GS71
Replications	2	21.4	24.8	4.5	26.8	23.2	8.3
Genotypes	9	527.6**	74.7*	13.0**	550.6***	80.5*	14.7**
GCA	3	720.4**	69.1	4.6	730.3**	72.9	6.4
SCA	6	431.2**	76.6*	17.2**	460.8**	84.3*	18.9**
Error	18	98.1	23.5	3.3	99.5	26.6	2.7
CV%		15.3	17.3	14.4	29.6	7.4	1.9

*, **, *** show significance level at 0.05 and 0.001 probability, respectively.

The coefficients of variation values were not high for both methods (Table 2). These values indicate that reliable information can be obtained to evaluate membrane thermal stability of the leaf samples taken from small plots. Chil's had the highest membrane stability at the GS14 and GS32 stages (Table 3). But, it had the lowest measurement values at the GS71 stage. Similar pattern was observed for Chil's x Seri-82 F_2 populations. The parent Genç 99 and 84ÇZT04 had significantly lower MTS and RI values at GS14 than Chil's and Seri-82 and both were characterized as heat sensitive according to membrane stability values. There were no significant differences between the F_2 progenies and the parents, but the F_2 means had lower MTS and RI values than their parents at the GS14 and GS32 stages. However, the F_2 progenies had larger membrane stability values than their respective parents at the GS71 stage.

With plant growth a decrease was observed in both MTS and RI (Table 3). When MTS and RI were evaluated simultaneously, similar tendency was observed throughout all growing stages. This was supported by significant positive association between MTS and RI (Table 4). Correlation coefficients between membrane stability values at early development, GS14 and GS32, were very high and positive. However, the correlations between the values at pre-anthesis stages and at the beginning of early milk development stage (GS71) were negative.

Table 3. Mean membrane thermal stability (MTS) and relative injury (RI) values for four wheat parents and their F_2 populations at different growing stages.

	MTS			RI		
Parents	GS14	GS32	GS71	GS14	GS32	GS71
(1) Genç 99	53.8	28.5	11.7	55.1	30.2	13.1
(2) 84ÇZT04	55.3	29.8	10.7	57.1	32.6	11.9
(3) Chil's	90.8	36.2	9.5	92.5	37.7	10.6
(4) Seri 82	69.9	28.5	10.3	70.8	30.7	11.8
Mean	67.5	30.8	10.6	68.9	32.8	11.9
F_2 Populations						
1 x 2	61.1	18.6	13.4	62.7	20.4	14.3
1 x 3	49.3	26.0	15.8	50.5	28.6	17.4
1 x 4	73.1	26.7	13.9	74.2	29.1	15.2
2 x 3	50.1	22.3	15.3	50.7	24.2	16.7
2 x 4	69.6	31.0	11.9	72.1	34.5	13.3
3 x 4	75.3	32.2	12.7	77.7	35.1	12.3
Mean	63.1	26.1	13.8	64.7	28.7	14.9
General mean	64.8	28.0	12.5	66.3	30.3	13.7
LSD $_{(0.05)}$	16.9	8.3	3.1	17.1	8.9	2.8

Table 4. Correlation coefficients between MTS and RI measurements and grain yield.

		MTS			RI		
		GS14	GS32	GS71	GS14	GS32	GS71
MTS	GS14	1	0.66*	-0.59	0.99**	0.63	-0.66*
	GS32		1	-0.67*	0.66*	0.99**	-0.69
	GS71			1	-0.59	-0.64*	0.96**
RI	GS14				1	0.64*	-0.67*
	GS32					1	-0.67*
Grain yield		-0.15	-0.57	0.68*	-0.20	-0.54	0.73*

* and **, significant at the 0.05 and 0.01 probability levels, respectively.

Significant correlations between grain yield and membrane stability values were observed at GS71. The correlation coefficients between grain yield and membrane values were not significant at GS14 and GS32. Also, significant positive correlation was found between membrane measurements and grain number per spike at the GS14 developmental stage (data not shown). Agronomic traits excluding grain yield, given in Table 1 were not significantly associated to membrane values at GS71 (data not shown).

GCA and SCA effects of MTS and RI measurements were of mostly similar (Table 5 and 6). Positive values of the GCA and SCA effects, determined in all stages of both measurement methods, contributed to membrane stability, while negative effects of GCA and SCA indicated contribution to membrane instability. Genç 99 was determined to have positive GCA effects on heat tolerance only at GS71 (Table 5). 84ÇZT04 had decreasing GCA effects at all stages. The GCA effects of Chil's which pointed to its heat tolerance were stable across all growing stages.

In the F_2 progenies, positive and negative SCA effects were determined across all growing stages (Table 6). Chils x Seri-82 had significant positive SCA effects at the GS14 and GS32 stages and negative SCA effects at the GS71 stage. Genç-99 x Chil's population had significant heat tolerance SCA effects at only GS71 stage.

Table 5. Estimates of general combining ability effects (GCA) for membrane thermal stability (MTS) and relative injury (RI) of wheat parents.

	MTS			RI		
Parents	GS14	GS32	GS71	GS14	GS32	GS71
(1) Genç 99	-5.50 *	-1.93	0.65	-5.68 *	-2.19	0.79 *
(2) 84ÇZT04	-5.45 *	-1.38	-0.11	-5.34 *	-1.20	-0.04
(3) Chil's	5.33 *	2.11 *	0.04	5.36 *	1.95	-0.12
(4) Seri 82	5.61 *	1.18	-0.56	5.65 *	1.44	-0.65

*, significant at the 0.05 probability level.

Table 6. Estimates of specific combining ability effects (SCA) for membrane thermal stability (MTS) and relative injury (RI) of F_2 populations of wheat.

	MTS			RI		
F_2 Populations	GS14	GS32	GS71	GS14	GS32	GS71
1 x 2	7.17	-6.12 *	0.34	7.37	-6.55*	-0.13
1 x 3	-15.30 **	-2.19	2.55 *	-15.5**	-1.46	3.11**
1 x 4	8.18	3.89	-0.79	8.05	3.78	-0.78
2 x 3	-14.63 **	-6.36 *	2.81 **	-15.65**	-6.86*	3.13**
2 x 4	6.03	7.86 **	-1.51	6.88	8.96**	-1.36
3 x 4	14.73 **	4.72*	-2.29 *	15.75**	4.87*	-3.41**

* and **, significant at the 0.05 and 0.01 probability levels, respectively.

Discussion

The increase at the agronomic traits of spike kernel number and kernel weight of hybrid populations is in agreement with the study of Aydogan Ciftci and Yagdi (2007). Both MTS and RI have been used by different researchers to evaluate heat stress (Sairam and Srivastava 2001, Dhanda and Munjal 2006). The high correlation between same growing stages showed that either MTS or RI measurement can be reliably used to determine electrolytic conductivity of wheat genotypes. However, MTS can be preferred to RI to save from time and laboratory facilities. When comparing membrane measurements methods for GS14 and GS32, significant positive correlations were found between two methods (r^2=0.66 and 0.64 for MTS and RI, respectively) which indicates that the membrane measurements at the two different development stages were well associated. Similar associations were reported by Reynolds et al. (1994a). The significantly positive correlation between grain yield and membrane stability at the GS71 revealed that the measurements at the late growing stage would be more useful to detect intrinsic high yielding genotypes. Dhanda and Munjal (2006) reported significant positive correlation between MTS and grain yield at anthesis period. However, similar correlation was found at the GS71 in our study. Mean values of 10 wheat varieties collected from 16 different low humid environments indicated a positive correlation between yield and MTS (r^2=0.81**) (Reynolds et al. 2001). Also, membrane stability were significantly correlated with grain yield in experiments conducted at the International Center for Maize and Wheat Improvement (CIMMYT) which were conducted with 16 lines at six different heat-stressed environments using both seedlings and flag leaves, (Reynolds et al. 1994a).

Shanahan et al. (1990) obtained a significant increase in yield of spring wheat in hot locations by selection of membrane-thermostable lines, as determined by measurements on flag leaves at anthesis. In this study, significant positive correlation between grain yield and flag leaf membrane stability at the early milk stage (GS71) indicate that high membrane stability of at this stage resulted in higher grain yield. Similarly, the highest grain yield was obtained from the populations of Genç-99 x Chil's and 84ÇZT-04 x Chil's, which had highest membrane values at GS71.

Membrane stability potential of genotypes decreased towards the end of the crop life. Membrane instability at post-anthesis period (i.e. precisely at GS71 stage) might be resulted from the start of senescence processes. In a study conducted with both tetraploid and hexaploid wheat, membrane stability showed a decrease during the measurement stages of 60, 70 and 80 days after sowing under irrigated conditions (Chandrasekar et al. 2000). Decrease in MTS or heat sensitivity reflects the extent of lipid peroxidation caused by active oxygen species (Dhinsa et al. 1981). In a study, reduction in rice yields as a result of high night temperature was attributed to increased leaf electrolytic leakage (Mohammed and Tarpley 2009).

MTS and RI appear to be conditioned mainly by non-additive gene action for all measurements time. Ibrahim and Quick (2001) concluded that both the GCA and SCA effects for MTS at 8-10 day wheat seedling were significant, accounting for 44% and 19% of the total variability, respectively. The average difference between parents and their progenies was generally caused by transgressive segregation in all growing stage. Also, high heat tolerance mechanism of Genç-99 x Seri-82 and Chil's x Seri-82 populations which were obtained by crossing heat tolerant and heat sensitive parents can be explained by complementary gene action. Saadalla et al. (1990b) observed transgressive segregation in F_5 progeny means of relative injury values determined by MTS test, suggesting that the parent contributed different genes for heat tolerance. High grain yield capacity of Genç-99 x Chil's and 84ÇZT-04 x Chil's populations which characterized heat tolerance showed that promising heat tolerant lines can be selected in the early segregating populations without any decrease in grain yield. These results indicate that MTS or RI can be used as complementary tools in breeding programs for screening of heat tolerance potential in spring wheat and evaluation of genetic variation in membrane stability among genotypes.

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