Investigation the Effect of Abscisic Acid on Drought Stress Induction in Wheat Seedling

S. S. Moosavi, B. Y. Samadi, A. Zali, M. Ghannadha, M. Omidi and M. Naghavi

Agriculture College, Tehran University, Karaj, Iran, e-mail: ssmoosavi@ut.ac.ir

Abstract: Wheat is the most important plant that always has suffered from drought stress (Quarrie *et al*. 1980). Most research that has been done on drought stress in plant, show that ABA increases in plant cultures after stress (Quarrie *et al*. 1977). In this research we performed three separate experiments in a randomized complete block design with three replications. In the first experiment, the effect of PEG on six cultivars (Sardari, Azare2, Kavir, Tabasi, Gaspard and Meroa) was invested. We measured shoot length, root length, cleoptile length, root/shoot length ratio, root/cleoptile length ratio, shoot fresh weight, shoot dry weight, root fresh weight, relative water content, germination rate and germination percentage. Bases on the measured traits, Azare2 and Sardari were the most resistant and Gaspard was the most susceptible cultivar. In this experiment we used six levels of PEG and in the second experiment the same cultivars were used in field with and without stress in complete randomized block design and 4 replications in each condition. After harvesting performance also SSI, TOL, MP, STI, GMP and HARM were measured and used to introduce the most resistance and sensitive cultivars by cluster analysis. In third experiment we used six levels of PEG and four levels of ABA on Sardari and Gaspard and measured shoot length, root length, cleoptile length, root /shoot length ratio, root /cleoptile length ratio, shoot fresh weight, shoot dry weight, root fresh weight, relative water content, relative water and germination percentage .In third experiment there was significant difference among cultivars for PEG and there were not significant difference for ABA. Sardari cultivar responded better than Gaspard to PEG levels.

Keywords: ABA; PEG; wheat; drought stress

Abbreviate: ABA – abscisic acid; PEG – polyethylene glycol; RWC – relative water content; RW – relative water; S.L. – shoot length; R.L. – root length; C.L. – cleoptile length; R/S – root/shoot; R/C – root/cleoptile; S.F.W. – shoot fresh weight; S.D.W. – shoot dry weight; S.W.P. – shoot water percent; R.F.W. – root fresh weight; R.D.W. – root dry weight; R.W.P. – root water percent; G.S. – germination speed; G.S./D. – germination speed in day; G.P. – germination percent; RCBD – randomized complete block design

Wheat as the major crop in Iran and the world has always underground drought stress. Subjection a crop in critical conditions including drought stress causes some physiological, morphological and growth alterations which most of them are controlled by abscisic acid (Shinozaki *et al*. 1999; Zhang *et al.* 1990; Stewart *et al*. 1985). In fact that above alterations is mainly due to changes in transcription level of genes that eventually their final products response to drought or other environmental stress (Passious *et al*. 1996; Zeevaart *et al*. 1977). Most of researches on the drought resistants in crops demonstrate that ABA level is increased in drought conditions, suggestion the essential role of this plant hormone in response to drought (Zhang *et al*. 1989; Stewart *et al*. 1985). Most of genes which have studied so far are affected by ABA so that genes which their expression in drought stress conditions is governed by ABA are called ABA – dependent genes (Dodd *et al*. 1996; Larque-

Saavedra *et al*. 1976). It seems that cell plasmolysis and turgor reduction lead to ABA synthesis and subsequently affects different gene expression (Seo *et al*. 2000). Some studies show that there is no response to external ABA treatment in genes which are so-called active in plasmolysis (Beard *et al*. 1975; Harrison *et al*.1975). Poly Ethylene Glycol (PEG) is the most used material for drought stress simulation *in vitro* (Gul *et al*. 1979). Parma and Morer (1968) showed that PEG_{2000} simulates soil potential much better than NaCl. In an experiment on bread wheat cultivars under 5 osmotic level (0, –0.5, –1, –1.5 and –2 MPa) it was demonstrated that germination percentage and germination rate is higher in resistant cultivars in stress conditions that sensitive cultivars. Also root and shoot weights in all cultivars were decreased by decreasing osmotic potential (Baalbaki *et al*. 1999). Naylor and Garmu (1990) indicated that in deficit potential conditions, water entrance and diffusion in to root (radicle) is decreased. Hampson and Simpson (1990a) studied 6 cultivars of wheat and 10 varieties of *Triticale* using PEG_{8000} and found that germination percentage and root growth reduction was higher in –6 level rather than –3 level.

MATERIALS AND METHODS

This research was carried out in 3 separate experiments in laboratory and field situations in Agricultural College Karaj, University of Tehran. In first experiment was studied the effects of different level of PEG on 6 cultivars of Sardari, Azare 2, Kavir, Tabasi, Gaspard and Meroa by Using a factorial experiment base on CRDB in triplicate was studied. PEG level were 0, –2, –4, –6, –8, –10 bar. After proportion of different level of PEG in sterile distilled water under laminar flow air hood, a sterilized filter paper was placed in each Petri dish, then the seed were storied with an enough amount of hypochlorite Sodium (1%) for 5–7 min and 30 uniform and right seeds were placed in each Petri dish and a dose of 5^{cc} PEG solution was poured in each Petri dish. Finally after coding, Petri dishes were placed in 3 separate racks as 3 blocks in germinator in 20°C for a week. In each day the number of germinated seed was recorded and after 7 days other traits such as shoot length, root length, cleoptile length, root/shoot length ratio, root/cleoptile length ratio, shoot fresh weight, shoot dry weight, root fresh weight, relative water content, germination rate and germination percentage, were determined and analyzed.

In the second experiment the same cultivars were used in field with and without stress in CRBD and 4 replications. After harvesting performance also SSI, TOL, MP, STI, GMP and HARM were measured and used to introduce the most resistance and sensitive cultivars by cluster analysis.

In the third experiment the aim was to study the interaction of different level of PEG and ABA (0, 2, 4, 6 μmol/l) on two resistant (Sardari) and sensitive (Gaspard) cultivars selected from the above two experiments in addition to the effect of ABA on resistance induction. The selected cultivars were tested in triplication a factorial experiment based on CRBD. All stages were similar but in that here 24 different PEG and ABA solutions were used. Finally the same traits also relative water content and relative water were determined. We obtained RWC and RW so as:

$$RWC = \frac{\text{(fresh weight)} - \text{(dry weight)}}{\text{(saturate weight)} - \text{(dry weight)}}$$

$$RW = \frac{\text{(fresh weight) (dry weight)}}{\text{(fresh weight)}}$$

RESULTS AND DISCUSSION

In the first experiment there was a significant different among cultivars for the major traits suggesting a diversity in these traits (Table 1). Among different levels of PEG for most traits except root/shoot and root/coleoptile length ratio was a significant difference indicating the different effect of different PEG level on the growth and development of the 6 wheat cultivars. As given in this table, the interaction between different PEG levels and cultivars in not significant for any traits which demonstrates a uniform trend in trait alterations in different drought levels. Mean comparison show that for the trait shoot length, the cultivars of Gaspsrd and Tabasi are classified in group B and the other in group A. This trend meets other traits. It should be noted that the cultivars Azar 2, Sardari and Kavir from all measured traits stand of view except germination rate per day are grouped together suggesting a similar response to different levels of PEG in these cultivars (Table 2). Cluster analyzing also showed similar results, i.e. cultivars Azar 2 , Sardari and Kavir nested in one cluster and Tabasi, Meroa and Gaspard in the other cluster, so that Sardari and Gaspard were recognized as the

Table 1. Analysis of variance for first experiment

S.O.V.	D.F.	MS													
		G.P.	G.S./D.	G.S.	R. W. P.	R.D.W. (g)	R.F.W. (g)	S.W.P.	S.D.W. (g)	S.F.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
rep	2	436.17**	0.80	23.48**	934.45**	0.041**	0.204**	48.64^{ns}	0.038**	0.211**	1.45^{ns}	0.174^{ns}	51.1*	9.54^{ns}	12.25**
Cultivar	5	366.01**	6.81**	1.94**	78.33^{ns}	0.053**	0.104**	158.54^{ns}	0.025**	0.064^{ns}	2.7^{ns}	0.029^{ns}	48^{ns}	9.80**	4.43**
PEG	5	2704.5**	92.6**	24.32**	179.32*	0.39**	0.912**	413.32*	0.67**	3.03**	4.35^{ns}	0.41^{ns}	1031.6**	92.2**	133.55**
Cul. × PEG	25	35.78^{ns}	0.62^{ns}	0.21^{ns}	78.68^{ns}	0.006^{ns}	0.029^{ns}	135.18^{ns}	0.008^{ns}	0.320^{ns}	1.85^{ns}	0.06^{ns}	15.88^{ns}	3.41^{ns}	1.66^{ns}
Error	70	29.97^{ns}	0.46^{ns}	0.29^{ns}	57.48^{ns}	0.004^{ns}	0.028^{ns}	117.6^{ns}	0.005^{ns}	0.033^{ns}	1.13^{ns}	0.11^{ns}	16.14^{ns}	2.06^{ns}	0.88^{ns}
C.V. (%)		23.91	25.5	19.69	9.68	28.6	21.88	13.36	20.5	25.78	17.93	28.73	18.20	26.85	21.74

**significant for α = 0.01, *significant for α = 0.05 and ^{ns}= not significant

Table 2. Mean comparison for cultivars with different traits in first experiment

Experimental treatments		Means													
		G.P.	G.S./D.	G.S.	R.W.P.	R.D.W. (g)	R.F.W. (g)	S.W.P.	S.D.W. (g)	S.F.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
Cultivars	Sardari	44.27^{A}	3.85^{A}	3.16^{A}	74.61^{B}	0.30^{A}	0.86^{AB}	81.3^{AB}	0.38^{A}	0.55^{A}	3.39^{A}	1.21^{A}	3.6^{A}	6.2^{A}	4.98^{A}
	Azar 2	16.03^{C}	2.29^{D}	2.41^{B}	81.94^{A}	0.17^{B}	0.76^{AC}	87.002^{A}	0.31^{BC}	0.51^{AB}	2.17^{B}	1.07^{A}	3.76^{A}	5.39^{AB}	4.46^{A}
	Kavir	25.65^{A}	3.42^{AB}	3.01^{A}	^{AB} 80.003	0.29^{A}	0.87^{A}	76.17^{B}	0.38^{A}	0.53^{AB}	3.1^{AB}	1.17^{A}	2.65^{A}	5.72^{A}	4.46^{A}
	Tabasi	21.53^{B}	2.83^{C}	2.47^{B}	78.85^{AB}	0.21^{B}	0.7^{C}	79.86^{AB}	0.30^{C}	0.45^{AB}	2.34^{B}	1.13^{A}	0.95^{AB}	4.24^{C}	3.79^{B}
	Gaspard	19.87^{B}	2.42^{CD}	2.46^{B}	77.43^{AB}	0.19^{B}	0.7^{C}	79.61^{AB}	0.31^{C}	0.42^{B}	2.71^{AB}	1.19^{A}	0.51^{B}	4.7^{BC}	3.67^{B}
	Meroa	29.84^{A}	3.36^{B}	2.94^{A}	76.95^{AB}	0.27^{A}	0.74^{BC}	82.82^{AB}	0.36^{AB}	0.57^{A}	3.08^{AB}	1.15^{A}	2.18^{AB}	5.8^{A}	4.52^{A}

Table 3. Mean comparison for PEG levels with different traits in first experiment

Experimental treatments		Means													
		G.P.	G.S./D.	G.S.	R.W.P.	R.D.W. (g)	R.F.W. (g).	S.W.P.	S.D.W. (g)	S.F.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
PEG	0 bar	35.01 ^{A}	5.97 ^{A}	4 ^{A}	81.08 ^{A}	0.38 ^{A}	0.97 ^{A}	87.11 ^{A}	0.55 ^{A}	1.06 ^{A}	3.08 ^{A}	0.93 ^{B}	17.3 ^{A}	7.01 ^{A}	7.3 ^{A}
	−2 bar	33.35 ^{A}	4.92 ^{B}	3.7 ^{A}	80.95 ^{A}	0.39 ^{A}	0.94 ^{AB}	82.37 ^{AB}	0.51 ^{A}	0.85 ^{B}	3.25 ^{A}	1.18 ^{A}	18.94 ^{A}	7.82 ^{AB}	6.7 ^{A}
	−4 bar	29.6 ^{B}	3.78 ^{C}	3.25 ^{B}	75.6 ^{AB}	0.31 ^{B}	0.89 ^{AB}	79.22 ^{B}	0.44 ^{B}	0.63 ^{C}	2.73 ^{AB}	1.24 ^{A}	17.52 ^{A}	6.72 ^{AB}	5.66 ^{B}
	−6 bar	22.71 ^{C}	2.42 ^{D}	2.80 ^{C}	75.19 ^{AB}	0.21 ^{C}	0.83 ^{B}	75.84 ^{B}	0.30 ^{C}	0.33 ^{D}	2.14 ^{B}	1.27 ^{A}	13.5 ^{B}	4.98 ^{C}	3.96 ^{C}
	−8 bar	11.59 ^{D}	0.82 ^{E}	1.62 ^{D}	73.01 ^{B}	0.092 ^{D}	0.63 ^{C}	70.03 ^{C}	0.16 ^{D}	0.11 ^{E}	2.12 ^{B}	1.29 ^{A}	4.26 ^{C}	3.56 ^{D}	1.64 ^{D}
	−10 bar	5.01 ^{E}	0.26 ^{F}	1.08 ^{E}	72.02 ^{B}	0.052 ^{D}	0.39 ^{D}	69.01 ^{C}	0.08 ^{E}	0.053 ^{E}	2.01 ^{C}	1.31 ^{A}	1.15 ^{D}	1.95 ^{E}	0.64 ^{E}

Table 4. Drought stress indexes for different cultivars in second experiment

Cultivars	Normal yield (kg)	Stress yield (kg)	SSI	TOL	MP	STI	GMP	HARM
Sardari	374.62	306.70	0.3666	67.92	340.66	0.504	338.96	337.27
Azar 2	384	230.36	0.8091	153.64	307.18	0.388	297.41	287.96
Kavir	464.47	184.85	1.2174	279.61	324.66	0.3769	293.02	264.46
Tabasi	740.37	305.94	1.1866	434.43	523.15	0.9976	475.93	432.97
Gaspard	462.12	226.97	1.0290	235.14	344.55	0.4604	323.87	304.43
Meroa	438.12	192.81	1.1322	245.30	315.47	0.3708	290.65	267.784

Table 5. Analysis of variance for third experiment

S.O.V.	D.F.	MS									
		R.W.	R.W.C.	G.P.	R.D.W. (g)	S.D.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
rep	2	0.019**	0.004**	260.77ns	0.002ns	0.007ns	0.002ns	0. 009ns	0.001ns	3.09ns	0.03ns
Cultivars	1	0.077**	0.092**	5929**	0.042**	0.005*	0 .001ns	0.0006ns	0.69*	179.5**	0.49*
PEG (drought)	5	0.0046ns	0.005ns	17989.7**	0.107**	0.10**	1.89**	2.33**	26.82**	777.3**	18.11**
ABA	3	0.0039ns	0.0052ns	204.55ns	0.001ns	0.001ns	0.03ns	0.01ns	0.105ns	3.83ns	0.07ns
Cul. × PEG	5	0.004ns	0.0045ns	296.73ns	0.005**	0.002ns	0.12**	0.90**	0.189ns	26.78**	0.10ns
Cul. × ABA	3	0.0046ns	0.0045ns	57ns	0.0004ns	0.001ns	0.005ns	0.005ns	0.093ns	5.63ns	0.06ns
PEG × ABA	15	0.0039ns	0.0052ns	248.91*	0.001ns	0.001ns	0.031ns	0.03ns	0.068ns	2.49ns	0.064ns
Cul. × PEG × ABA	15	0.0035ns	0.0045ns	277.53ns	0.0003ns	0.0008ns	0.014ns	0.01ns	0.127ns	2.52ns	0.105ns
Error	94	0.00007ns	0.00013ns	131.86ns	0.001ns	0.001ns	0.02ns	0.02ns	0.105ns	2.54ns	0.074ns
C.V. (%)		5.3	6.7	16.9	28.34	25.01	9.85	10.1	16.08	16.5	15.22

**significant for α =0.01, *significant for α = 0.05 and ns = not significant

Table 6. Mean comparison for cultivars with different traits in third experiment

Experimental treatments		Means									
		R.W.	R.W.C.	G.P.	R.D.W. (g)	S.D.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
Cultivars	Sardari	1.51 B	1.5 B	74.38 A	0.106 A	0.081 A	1.45 A	1.42 3A	2.08 A	8.10A	1.85 A
	Gaspard	1.56 A	1.56 A	61.55 B	0.072 B	0.068 B	1.44A	1.428 A	1.94 B	8.54 B	1.73 B

Table 7. Mean comparison for ABA levels with different traits in third experiment

Experimental treatments		Means									
		R.W.	R.W.C.	G.P.	R.D.W. (g)	S.D.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
ABA	0 μ mol	1.54 ^{A}	1.535 ^{A}	70.22 ^{A}	0.098 ^{A}	0.077 ^{A}	1.49 ^{A}	1.41 ^{A}	1.95 ^{A}	9.82 ^{A}	1.76 ^{A}
	2 μ mol	1.52 ^{A}	1.53 ^{A}	69.77 ^{A}	0.09 ^{A}	0.077 ^{A}	1.45 ^{A}	1.42 ^{A}	1.06 ^{A}	10.04 ^{A}	1.58 ^{A}
	4 μ mol	1.51 ^{A}	1.51 ^{A}	66.44 ^{A}	0.081 ^{A}	0.065 ^{A}	1.41 ^{A}	1.4 ^{A}	1.05 ^{A}	9.35 ^{A}	1.81 ^{A}
	6 μ mol	1.49 ^{A}	1.50 ^{A}	65.44 ^{A}	0.086 ^{A}	0.079 ^{A}	1.42 ^{A}	1.41 ^{A}	1.98 ^{A}	9.42 ^{A}	1.75 ^{A}

Table 8. Mean comparison for PEG levels with different traits in third experiment

Experimental treatments		Means									
		R.W.	R.W.C.	G.P.	R.D.W. (g)	S.D.W. (g)	R/C	R/S	C.L. (mm)	R.L. (mm)	S.L. (mm)
PEG	0 bar	1.53 ^{A}	1.537 ^{A}	84.33 ^{A}	0.11 ^{B}	0.137 ^{B}	1.06 ^{D}	1.07 ^{D}	3.24 ^{A}	13.81 ^{B}	2.9 ^{A}
	–2 bar	1.52 ^{A}	1.535 ^{A}	91 ^{A}	0.16 ^{A}	0.163 ^{A}	1.23 ^{C}	1.22 ^{C}	3.06 ^{A}	15.59 ^{A}	2.57 ^{B}
	–4 bar	1.50 ^{A}	1.532 ^{A}	87.16 ^{A}	0.15 ^{A}	0.091 ^{C}	1.44 ^{B}	1.44 ^{B}	2.44 ^{B}	13.72 ^{B}	2.09 ^{C}
	–6 bar	1.49 ^{A}	1.531 ^{A}	74.16 ^{A}	0.07 ^{C}	0.034 ^{D}	1.71 ^{A}	1.71 ^{A}	1.55 ^{C}	7.87 ^{C}	1.44 ^{D}
	–8 bar	1.43 ^{B}	1.48 ^{B}	50.5 ^{C}	0.02 ^{D}	0.014 ^{E}	1.73 ^{A}	1.73 ^{A}	1.06 ^{D}	4.24 ^{D}	1.05 ^{E}
	–10 bar	1.41 ^{B}	1.47 ^{B}	20.66 ^{D}	0.003 ^{E}	0.008 ^{E}	1.75 ^{A}	1.75 ^{A}	0.71 ^{E}	1.72 ^{E}	0.71 ^{E}

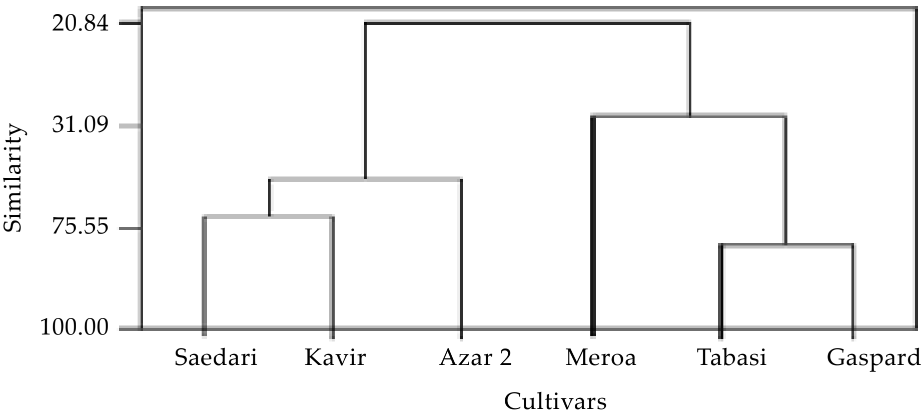

Figure 1. Cluster analysis of six cultivars in first experiment

most resistant and sensitive cultivars respectively (Figure 1). Mean comparison of different PEG levels for the traits show that with increasing PEG level (up to –10 bars), a decrease is seemed in all traits except root/shoot length ratio. Therefore it is concluded that with increasing drought level, the crop increases its root growth to shoot ratio to survive the stress conditions (Table 3). Drought indexes and cluster analysis of the second experiment also showed that Sardari cultivar was the most resistant and two cultivars Tabasi and Gaspard were the most sensitive (Table 4 and Figure 2). Overally Saedari and Gaspard respectively were selected as the most resistant and sensitive cultivars.

In the first and second experiment, Sardai and Gaspard cultivars were selected and entered the third experiment. For this stage the goal was to study the inductive effect of ABA on drought stress in different levels of PEG and the most resistant and sensitive cultivars. All cultivars regarding all traits except root/shoot and root/coleoptile length ratio were significant, suggesting traits diversity. For the different levels of PEG there was shown significant difference for all traits except the RWC and RW of seedlings. For the different levels of ABA there was no significant difference for any traits indicating lack of hormonal effect on drought resistance induction. Hence different level of this hormone had no significant effect on the traits also drought resistance induction. The interaction of cultivar and drought was significant for only such traits as root length, root/shoot, root/coleoptile length ratio and root dry weight. The interaction of cultivar and ABA was not significant for any trait suggesting uniform alteration in different level of ABA. Interaction between drought and ABA was significant only for germination percentage. The triple interaction that is cultivar, ABA and drought was not significant for any trait (Table 5). Mean comparison results show that for all traits except RWC

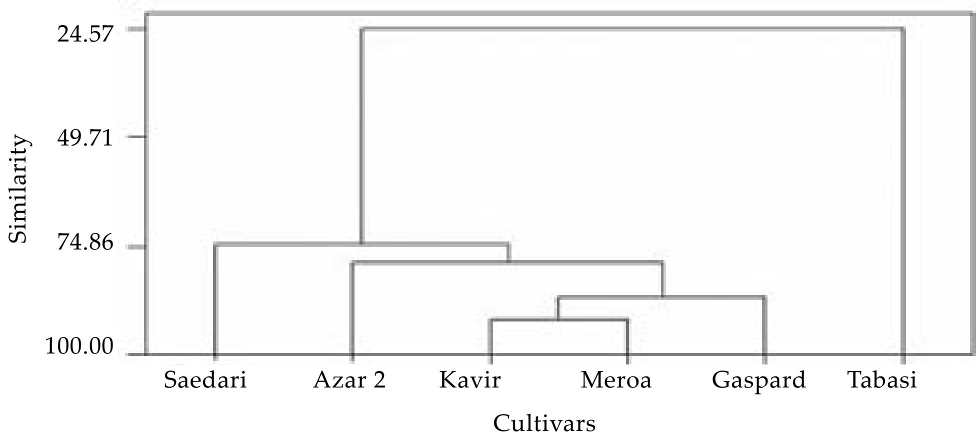

Figure 2. Cluster analysis of six cultivars in second experiment

and RW the Sardari cultivar is classified in group A which indicates its better response to drought stress than Gasper (Table 6). It was considered that for different levels of ABA, there was no significant difference for any traits showing no effect of ABA on the traits(Table 7). In relation to different levels of PEG, it was observed that increasing drought level had a reducing effect on most traits except root/shoot and root/coleoptile length ratio and for these two traits a reverse effect, so that these two traits showed an increase with increasing drought level showing much more relative growth of root/shoot in drought condition (Table 8).

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References

Beardsell M.F., Cohen D. (1975): Relationships between leaf water status, abscisic acid levels, and stomata resistance in maize and sorghum. Plant Physiology, **56**: 207–212.

Baalbaki R.Z., Zurayk R.A., Bleik M.M., Talhouk S.N. (1999): Germination and seeding development of drought tolerant and susceptible wheat under moisture stress. Seed Science and Technology, **27**: 291–302.

Davies W.J., Zhang J. (1991): Root signals and the regulation of growth and development of plants in drying soil. Annual Review of Plant Physiology and Plant Molecular Biology, **42**: 55–76.

Dodd I.C., Davies W.J. (1996): The relationship between leaf growth and ABA accumulation in the grass leaf elongation zone. Plant Cell and Environment, **19**: 1047–1056.

Gul A., Allen R.E. (1979): Stand establishment of wheat line under different levels of water potential. Crop Science, **16**: 611–615.

Hampson C.R., Simpson G.M. (1990): Effect of temperature, salt, and osmotic potential on early growth of wheat (*Triticum aestivum*). I. Germination. Canadian Journal of Botany, **68**: 524–528.

Harrison M.A., Walton D.C. (1975): Absicisic acid metabolism in water stressed bean leaves. Plant Physiology, **56**: 250–254.

Keller F., Ludlow M.M. (1993): Carbohydrate metabolism in drought-stressed leaves of pigeonpea (*Cajanus cajan* L.). Journal of Experimental Botany, **44**: 1351–1359.

Larque-Saavedra A., Wein R.L. (1976): Studies on plant growth regulation substances. XLII. Abscisic acid as a genetic character related to drought tolerance. Annals of Applied Biology, **83**: 291–297.

Naylor R.E.L., Gurmu M. (1990): Seed vigor and water relate in wheat. Annals of Applied Biology, **117**: 441–445.

Passious B.J. (1996): Drought and drought tolerance. Plant Growth Regulation, **20**: 79–83.

Quarrie S.A. (1980): Genotypic differences in leaf water potential, abscisic acid and praline concentrations in spring wheat during drought stress. Annals of Botany, **46**: 383–394.

Quarrie S.A., Jones H.G. (1977): Effects of abscisic acid and water stress on development and morphology of wheat. Journal of Experimental Botany, **25**: 192–203.

Shinozaki K., Yamaguchi- Shinozaki K. (1997): Gene expression and signal transduction in wheat stress response. Plant Physiology. **115**: 327–334.

Seo M., Peeters A.J. M., Koiwai H., Oritani T., Marion-Poll A., Zeevaart J.A.D., Koornneef M., Kamiya Y., Koshiba T. (2000). The Arabidopsis aldehyde oxidase 3 (AAO3) gene product catalyzes the final step in abscisic acid biosynthesis in leaves. Proc. Natl. Acad. Sci. USA 97, 12908–12913.

Stewart C.R., Voetberg G. (1985): Relationship between stress- induced ABA and praline accumulations and ABA- induced praline accumulation in exised barley leaves. Plant Physiology, **79**: 24–27.

Zeevaart J.A.D. (1977): Sites of abscisic acid synthesis and metabolism in *Ricinus communist* L. Plant Physiology, **59**: 788–791.

Zhang J., Davies W.J. (1989): Abscisic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. Plant Cell and Environment, **12**: 73–81.

Zhang J., Davies W.J. (1990): Changes in the concentration of ABA in the xylem sap as a function of changing soil water status can account for changes in leaf conductance and growth. Plant Cell and Environment, **13**: 277–285.