Drought and Salinity Stress Responses in Wheat (*Triticum aestivum* L.): Activation of Antioxidative Defense and Accumulation of Stress Responsive Metabolites

B. Pradhan and U. Chakraborty*

Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Siliguri, Darjeeling, West Bengal (734 013), India

Article History

Manuscript No. c421
Received in 28th September, 2012
Received in revised form 25th May, 2013
Accepted in final form 28th June, 2013

Correspondence to

**E-mail*: chakrabortyusha@hotmail.com

Keywords

Wheat, drought, lipid peroxidation, antioxidative enzymes, antioxidants

Abstract

Nine different wheat (*Triticum aestivum* L.) varieties- Mohan Wonder (MW), Kedar (KD), Gayetri (GY), Gandhari (GN), Kaweri (KW), PBW 343, UP 2752, Sonalika (SO), LV were subjected to drought stress for 3, 6 and 9 days and salt stress of 50 mM, 100 mM and 200 mM. A general decrease was seen in the activity of catalase and superoxide dismutase during both stresses in MW, GY, LV and SO whereas there was an initial enhancement in case of other cultivars. The activities of peroxidase and glutathione reductase showed a general increase in case of all varieties following drought and salt stress respectively but the later stages showed a decrease in case of MW, GY, LV and SO with the increase in the duration of stress. Ascorbate peroxidase showed a steep rise in its activity with the onset of stress followed by a decline when the duration and severity of stress increased. There was an increase in the accumulation of H_2O_2, lipid peroxidation and decrease in MSI in case of MW, GY, and LV and SO in the leaf following stress and a concentration dependent increase in H_2O_2 staining was observed in the leaf evident as brown coloured spots due to DAB polymerization in the stressed leaf in comparison with the control plants. Proline, total carbohydrates, starch, phenol and ascorbate content increased with increase in the period of water stress. The accumulation of total antioxidant and carotenoid showed an initial enhancement whereas total chlorophylls showed a general decline during water stress. Results of the present study indicate that out of the nine tested cultivars- KD, GN, KW showed the highest tolerance to the stress followed by PBW 343, UP 2752 and the other four showed were susceptible to drought and salinity stress.

1. Introduction

Drought and salinity stress affects morphological, physiological, biochemical and molecular processes in plants resulting in growth inhibition, stomata closure with consecutive reduction of transpiration, decrease in chlorophyll content and inhibition of photosynthesis and protein changes (Lawlor and Cornic, 2002; 2003; Zhu, 2002). Plants have both enzymatic and non-enzymatic antioxidant system to protect cells from oxidative damage to keep the levels of active oxygen species under control in terms of either decrease or increase in the levels of antioxidative enzymes like peroxidase (POX), superoxide dismutase (SOD), ascorbate peroxidase (APOX), catalase (CAT) and glutathione reductase (GR), enhanced levels of non-enzymatic system like ascorbate, carotenoids, phenols and the accumulation of stress metabolites like proline, carbohydrates (Chakraborty and Pradhan, 2011). Mittler (2002) suggested that due to the short living period of ROS, the damage effects are usually restricted at the sites of their production. In this respect, the antioxidant protection in plant cells is complex and highly compartmentalized, comprising enzymatic and non-enzymatic components. Wheat is one of the most important cultivated cereals of the world. In different parts India, productivity is affected by drought as well as salinity stress and the selection of drought or salt-resistant varieties become essential. In our study, an attempt has been made to study a comparative account of the plant to drought as well as salt induce stress in nine varieties of wheat with special emphasis on the role of antioxidants in protective mechanisms.

2. Material and Methods

2.1. Plant material, experimental conditions

Seeds of commercially relevant lines of nine wheat (*Triticum aestivum* L.) varieties (KW, LV, MW, GY, GN, KD, UP 2752, PBW 343 and SO) were selected for experimental purposes.

The seeds were surface sterilized for 3 minutes with 0.1% (w/v) $HgCl_2$ solution, washed twice with sterile double-distilled water and then transferred to petriplates maintaining aseptic conditions to avoid contamination. One-week-old seedlings were selected and transferred to earthen pots with soil containing a suitable amount of manure and the pots were labelled. To impart drought stress, watering of the plant was completely withheld for the test period, when the plants were 1 month old and for salt stress one month old plants were treated with 50 mM, 100 mM and 200 mM of sodium chloride (NaCl). For drought, sampling was done on 3rd, 6th and 9th day and for salinity stress on 1st and 3rd day of stress. In all estimations, sampling was also done at zero day of drought, which was considered as control.

2.2. Extraction and antioxidant enzyme assay

For extraction of enzymes, leaves from wheat seedlings were homogenized in 5 mL of ice-cold 50 mM sodium phosphate buffer, pH 7.2, containing 1% (w/v) polyvinylpolypyrrolidone using liquid nitrogen in a chilled mortar and pestle. The homogenate was then centrifuged at 6700 g for 20 min at 48°C. The supernatant was used directly as crude extract for enzyme assays. Peroxidase (EC 1.11.17) activity was assayed spectrophotometrically at 460 nm by monitoring the oxidation of o-dianisidine in the presence of hydrogen peroxide (H_2O_2) (Chakraborty et al., 1993). Specific activity was expressed as mmol o-dianisidine mg protein^{-1} min^{-1}. Ascorbate peroxidase (EC 1.11.1.11) activity was assayed as a decrease in absorbance by monitoring the oxidation of ascorbate at 290 nm according to the method of Asada and Takahashyi (1987) with some modification. Enzyme activity was expressed as mmol ascorbate mg protein^{-1} min^{-1}. Catalase (EC 1.11.1.6) activity was assayed as described by Chance and Machly (1955) by estimating the breakdown of H_2O_2, which was measured at 240 nm. The enzyme activity was expressed as mmol H_2O_2 mg protein^{-1} min^{-1}. Glutathione reductase (EC 1.6.4.2) activity was determined by the oxidation of NADPH at 340 nm as described by Lee and Lee (2000). Enzyme activity was expressed as mmol NADPH oxidized mg protein^{-1} min^{-1}. Superoxide dismutase (EC 1.15.1.1) activity was assayed by monitoring the inhibition of the photochemical reduction of nitro blue tetrazolium according to the method of Dhindsa et al. (1981) with some modification. The absorbance of the samples was measured at 560 nm and 1 unit of activity was defined as the amount of enzyme required to inhibit 50% of the nitro blue tetrazolium reduction rate in the controls containing no enzymes. Protein contents in extracts were quantified following the method of Lowry et al. (1951), using bovine serum albumin as standard.

2.3. Extraction and estimation of non-enzymatic antioxidants, stress metabolites and total chlorophyll content

Carotenoids were extracted in methanol and, for the estimation; the method described by Lichtenthaler (1987) was used. Extraction was done in methanol and the extract was filtered. Absorbance of the filtrate was noted at 480, 663 and 645 nm in a VIS spectrophotometer (Systronics, India, Model 101) and the carotenoid content (mg g^{-1} f.m.) was determined by the formula as given below:

$$A_{480} - (1.144 \text{ X } A_{663} - 0.638\ A_{645}) \quad \text{..... (i)}$$

For the extraction and estimation of ascorbic acid (ascorbate) the method as given by Mukherjee and Chaudhuri (1983) was used and the absorbance was measured in spectrophotometer at 530 nm and the units were expressed in mg g^{-1}d.m. Total phenols were extracted from the leaves following the method described by Mahadevan and Sridhar (1982) and quantified (Bray and Thorpe 1954) using Folin-ciocalteu reagent and the absorbance was measured at 650 nm in colorimeter expressed as mg g^{-1} d.m. Proline was extracted from the leaves using 3% sulfosalicylic acid and free proline was estimated following the method of Bates et al. (1973) using ninhydrin reagent and the absorbance was measured 520 nm in colorimeter and the units were expressed in mg g^{-1} d.m. Total carbohydrates were extracted from leaves and roots by following the method of Plummer (1978) and the absorbance was measured at 620 nm in a colorimeter and the units were expressed as mg g^{-1} d.m. Total chlorophyll was extracted using methanol and estimated by the method as described by Harborne (1973) and the absorbance was recorded at 663 and 645 nm using a UV-VIS spectrophotometer and calculated using standard formula.

3. Results and Discussion

In this study a general decrease was seen in the activity of catalase (Figure 1) during both drought and salt stress in case of MW, GY, LV and SO whereas in case of KW, GN, UP2752, PBW 343 and KD an initial enhancement was seen. The activities of peroxidase (Figure 1) and glutathione reductase (Figure 2) showed a general increase in case of all varieties following drought and salt stress but the later stages showed a decrease in case of MW, GY, LV and SO with the increase in the duration of stress indicating their involvement in impartment of tolerance. Chakraborty et al. (2002) also reported that peroxidase activities increased initially in all tea cultivars following drought stress, but in tolerant cultivars it increased even with prolonged periods.

With prolonged stress the activity of superoxide dismutase during both drought and salt stress in case of MW, GY, LV and SO showed a continued decrease whereas in case of KW, GN, UP2752, PBW 343 and KD an initial enhancement was seen however the activities of ascorbate peroxidase showed a steep rise in its activity with the onset of stress followed by a decline when the duration and severity of stress increased i.e., 9th day

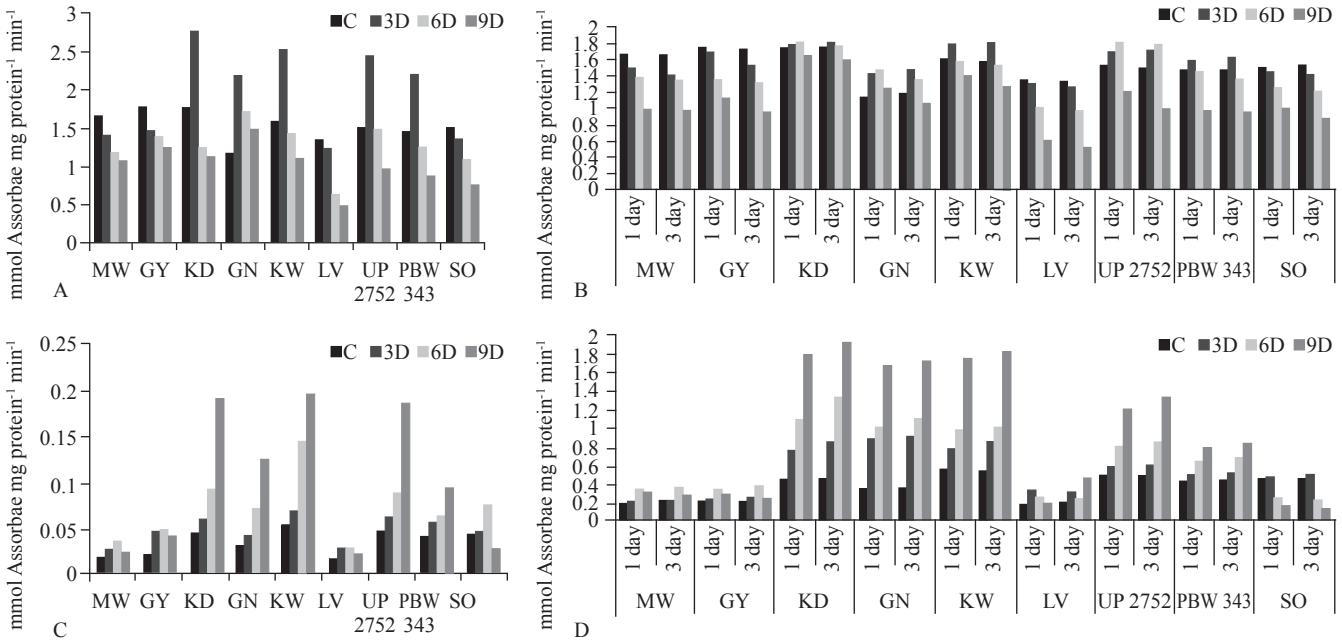

Figure 1: Antioxidative enzyme activities in drought (left) and salt (right) stressed nine wheat varieties. CAT (upper); PER (lower). C: control, 3, 6 and 9 days after withholding water and 50 mM, 100 mM and 200 mM of NaCl concentration

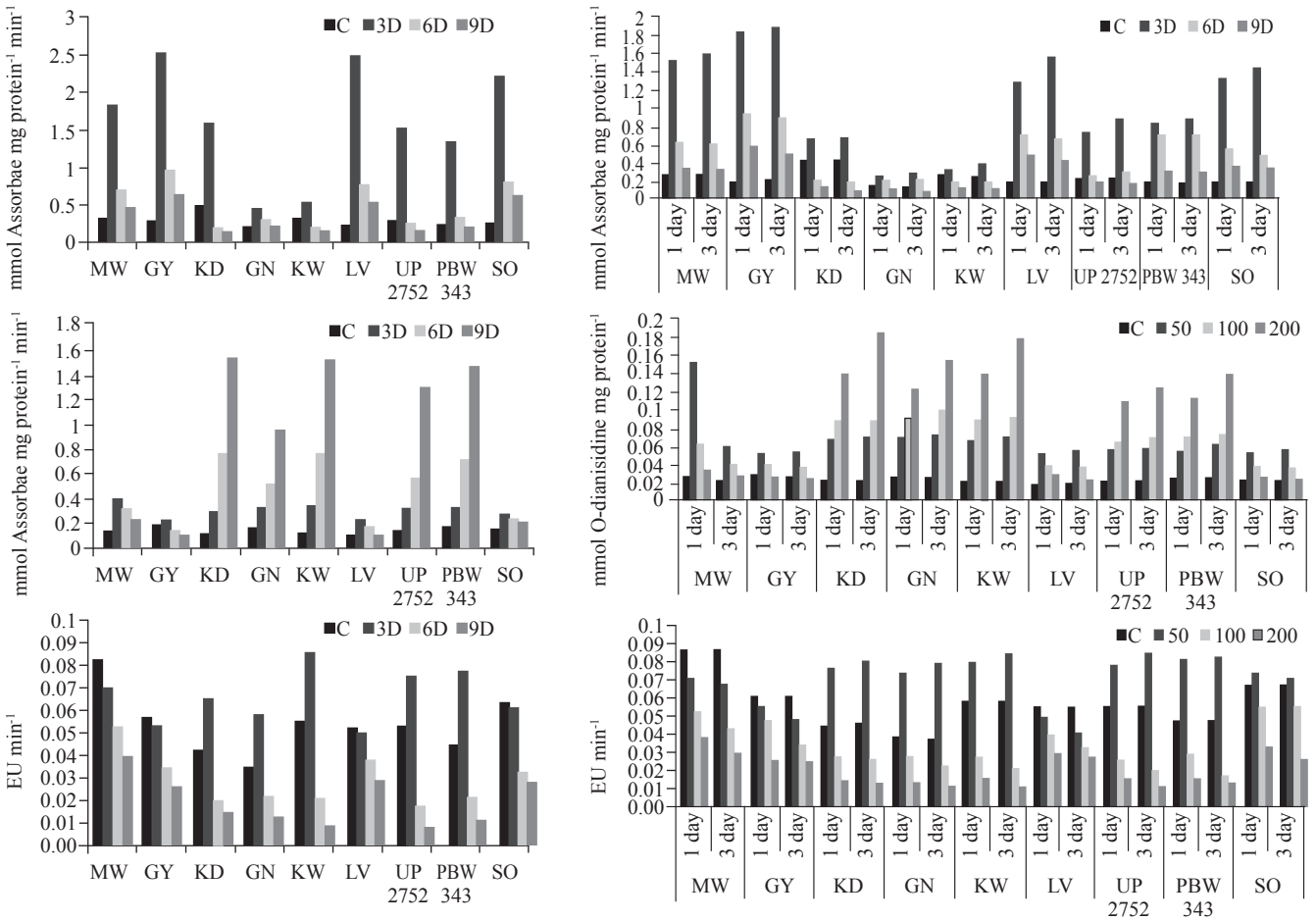

Figure 2: Antioxidative enzyme activities in drought stressed (left) and salt stressed (right) nine wheat varieties. APOX (upper); GR (middle); SOD (lower). C: control, 3, 6 and 9 days after withholding water and 50 mM, 100 mM and 200 mM of NaCl concentration

in case of drought and at 200 mM during the 3rd day in case of salt stress. Previous studies have also reported differential responses of genotypes to drought stress with respect to anti-oxidant enzymes (Dhanda et al., 2004; Nair et al., 2008).

Non-enzymatic antioxidants phenol, ascorbic acid and carotenoids increased significantly in all nine varieties in both drought (Table 1) and salt stress (Table 2). Accumulation of ascorbate was enhanced in all nine varieties even after 9 days of drought stress and even at 200 mM of salt stress on the 3rd day; carotenoids, however, decreased after 3 days of drought and at 100 mM of salt stress (3d) in varieties MW, GY, LV and SO and after 6 days of drought and at 200 mM (3d) in case of the other five varieties. Jaleel (2009) reported enhanced accumulation of ascorbic acid during drought stress in winter cherry (*Withania somnifera*).

In this study, the increase in ascorbate, along with glutathione

Table 1: Content of proline, phenol, ascorbate (mg g^{-1} dry matter), total chlorophyll and carotenoids (mg g^{-1} fresh matter) in the leaves of nine wheat varieties subjected to drought stress

Varieties	Treatment	Proline	Phenol	Ascorbate	Total chlorophyll	Carotenoids	Total Carbohydrate
MW	C	2.3	23.6	12.4	0.93	0.043	17.00
	3d	1.9	19.2	13.3	0.56	0.055	53.00
	6d	3.6	21.1	15.2	0.36	0.052	37.54
	9d	6.9	22.5	16.9	0.28	0.040	29.66
GY	C	2.2	28.3	9.4	1.01	0.044	28.34
	3d	2.0	17.3	15.4	0.56	0.067	54.00
	6d	4.8	20.9	16.6	0.45	0.041	33.34
	9d	5.8	21.3	17.9	0.41	0.030	28.34
KD	C	1.9	15.7	05.5	0.93	0.044	17.00
	3d	01.4	22.0	09.2	0.98	0.057	24.66
	6d	11.1	45.0	18.6	0.48	0.066	61.34
	9d	20.3	49.4	21.8	0.27	0.050	84.00
GN	C	2.0	29.8	9.4	1.05	0.042	26.00
	3d	2.6	42.3	10.8	1.21	0.063	43.34
	6d	6.0	43.1	11.2	0.65	0.067	77.00
	9d	10.6	46.7	16.3	0.57	0.052	109.0
KW	C	2.0	29.9	11.02	0.90	0.044	21.00
	3d	2.9	29.6	12.19	0.77	0.051	28.30
	6d	8.1	39.9	13.44	0.49	0.061	65.17
	9d	10.8	40.1	14.78	0.31	0.055	74.30
LV	C	1.7	38.4	9.98	1.22	0.048	11.12
	3d	1.6	39.6	9.90	0.41	0.049	58.00
	6d	5.0	44.0	10.10	0.31	0.038	31.12
	9d	5.1	34.0	11.30	0.29	0.029	27.55
UP 2752	C	2.5	33.6	12.11	2.30	0.050	13.71
	3d	2.3	31.0	12.98	0.75	0.062	58.43
	6d	9.8	46.8	14.90	0.63	0.052	33.71
	9d	11.2	30.1	15.51	0.62	0.038	29.52
PBW 343	C	1.7	36.8	11.96	1.73	0.047	18.31
	3d	2.3	33.6	13.15	0.86	0.048	25.00
	6d	7.5	40.8	13.51	0.57	0.042	48.77
	9d	11.9	29.1	15.81	0.39	0.037	50.10
SO	C	1.5	21.1	11.07	0.96	0.041	18.60
	3d	2.6	29.4	12.14	0.62	0.049	37.20
	6d	4.9	37.5	13.89	0.49	0.042	43.00
	9d	6.1	38.0	14.65	0.31	0.033	44.00

reductase, indicates involvement of the ascorbate-glutathione cycle as a predominant mechanism of oxidative stress detoxification. The accumulation of total phenol was greatly enhanced during both the stress with the increase being higher with increase of duration of water stress and concentration of salt in case of KW, GN, UP2752, PBW 343 and KD whereas in

Table 2: Content of proline, phenol and ascorbate (mg g^{-1} d.m.), total chlorophyll and carotenoids expressed in (mg g^{-1} f.m.) in the leaves of nine wheat varieties subjected to salt stress

Varieties	NaCl. (mM)	Proline		Phenol		Ascorbate		Total chlorophyll		Carotenoids		Total Carbohydrate	
		1d	3d	1d	3d	1d	1d	3d	3d	1d	3d	1d	3d
MW	C	2.3	2.3	23.6	23.9	12.4	0.043	0.043	12.5	0.93	0.93	17.0	19.0
	50	2.3	3.1	25.1	29.1	12.9	0.051	0.053	13.5	0.82	0.82	32.1	34.5
	100	3.7	3.9	24.3	26.1	15.8	0.049	0.051	13.8	0.81	0.79	49.0	43.0
	200	6.6	7.9	22.2	19.2	16.5	0.042	0.038	17.8	1.24	1.11	22.1	22.0
GY	C	2.2	2.1	28.3	28.4	09.4	0.044	0.044	09.3	0.10	0.99	28.3	29.2
	50	2.5	3.4	31.2	33.6	13.1	0.061	0.062	14.9	0.82	0.60	37.3	44.7
	100	3.8	4.0	28.9	26.5	15.5	0.042	0.043	15.6	0.81	0.80	50.0	39.1
	200	6.8	6.9	21.3	19.6	17.1	0.032	0.030	17.5	0.91	0.87	26.9	21.3
KD	C	01.9	02.0	15.7	16.0	05.5	0.044	0.045	5.40	0.93	0.92	17.0	16.9
	50	08.1	10.4	33.0	37.3	15.2	0.058	0.059	17.4	0.97	0.96	41.0	46.3
	100	13.6	15.3	31.1	32.3	16.8	0.069	0.072	18.5	0.70	0.68	54.2	59.0
	200	18.7	19.8	37.5	36.2	19.2	0.052	0.049	24.1	0.52	0.36	57.3	62.3
GN	C	02.0	01.9	29.8	30.2	09.4	0.042	0.043	09.5	1.05	1.11	26.0	25.9
	50	11.1	11.6	35.4	39.2	15.9	0.065	0.066	17.8	1.19	1.22	39.8	40.4
	100	13.4	18.1	31.0	29.6	20.1	0.069	0.071	22.2	0.65	0.58	55.1	58.3
	200	21.1	24.1	39.0	35.2	23.0	0.053	0.050	23.9	0.55	0.52	60.0	61.1
KW	C	02.0	02.0	29.9	28.9	11.0	0.044	0.045	11.4	0.90	0.91	21.0	21.5
	50	06.4	07.2	33.3	35.6	14.2	0.057	0.061	18.1	0.77	0.72	39.9	42.1
	100	11.0	13.3	29.1	31.1	19.4	0.064	0.065	21.0	0.53	0.54	51.2	55.0
	200	14.1	16.8	35.6	33.2	23.0	0.052	0.051	23.5	0.32	0.31	58.3	63.0
LV	C	1.7	1.6	38.4	38.0	9.90	0.048	0.049	10.0	1.22	1.23	11.1	12.0
	50	2.0	3.6	38.9	39.7	11.2	0.049	0.052	11.3	0.82	0.79	21.0	21.5
	100	3.5	3.7	36.7	37.0	13.9	0.039	0.037	14.5	0.75	0.66	33.0	38.2
	200	5.5	4.8	30.1	28.0	17.2	0.028	0.025	18.1	0.50	0.41	39.9	42.1
UP 2752	C	2.5	2.4	33.6	33.1	12.1	0.050	0.050	12.0	2.30	2.29	13.7	13.1
	50	4.3	4.6	34.8	35.1	13.5	0.058	0.059	14.5	0.81	0.73	11.1	12.0
	100	5.1	5.5	24.1	27.3	16.6	0.060	0.061	17.9	0.61	0.59	33.6	35.2
	200	7.8	9.7	29.3	25.4	21.2	0.041	0.043	23.0	0.59	0.57	33.0	38.2
PBW 343	C	1.7	1.7	36.8	36.1	11.9	0.047	0.048	12.0	1.73	1.72	18.3	17.0
	50	3.0	3.9	37.0	38.4	15.0	0.049	0.051	15.6	0.84	0.79	29.9	32.6
	100	4.5	4.9	26.4	32.6	19.2	0.056	0.062	19.4	0.61	0.57	48.2	39.8
	200	7.7	8.9	24.1	28.9	20.0	0.042	0.040	22.1	0.42	0.39	30.7	26.8
SO	C	1.5	1.5	21.1	20.8	11.4	0.041	0.041	11.3	0.96	0.95	18.6	17.9
	50	2.9	3.4	28.1	28.9	13.4	0.048	0.052	13.9	0.72	0.69	34.3	37.9
	100	5.6	5.9	26.0	26.5	17.1	0.043	0.041	18.5	0.51	0.49	48.7	41.5
	200	7.4	6.9	21.3	22.0	17.8	0.034	0.028	18.8	0.52	0.53	24.1	21.9

other varieties a decrease was observed during the later stages of stress. Leinhos and Bergman (1995) had studied the plant defense system against various types of stress with respect to the involvement of polyphenols as a response to stress and the results were in accordance with their findings. Chlorophylls, which are one of the first molecules to be affected by drought stress, showed a general decrease in all varieties in both drought (Table 1) and salt stress (Table 2). However, in tolerant varieties, there was an initial non significant increase. Free proline accumulation was enhanced in all nine varieties during prolonged drought stress (Table 1) and salt stress (Table 2) after an initial non-significant decrease. After 9 days of drought, proline content in KW, GN, UP2752, PBW 343 and KD was about 2.5 times higher than the other four varieties and about 3 times during both 1d and 3d of salt stress, although in control plants all varieties had more or less similar amounts. It is quite clear that proline accumulation during stress is one of the mechanisms of tolerance. Proline, which is usually considered as an osmoprotectant, may also be involved in reducing oxidative damage by scavenging the free radicals (Vendruscolo et al., 2007; Tatar and Gevrek, 2008).

4. Conclusion

The results of this study clearly indicate that both drought and salt stress induced oxidative damage in wheat varieties could be overcome by enhanced activities of antioxidative enzymes, as well as accumulation of other antioxidants such as ascorbic acid, carotenoids and phenol and also stress responsive metabolites like proline and carbohydrates. This was much more pronounced in five varieties KW, GN, UP2752, PBW 343 and KD than in MW, GY, LV and SO, which were probably more tolerant and therefore more protected from oxidative damage. Taking into consideration all the available data, it is concluded that whereas KW, GN, UP2752, PBW 343 and KD could be considered as tolerant, MW, GY, LV and SO were susceptible to both drought and salt stress.

5. Acknowledgements

The authors are grateful to University Grants Commission, New Delhi, India, for financial assistance.

6. References

Asada, K., Takahashi, M., 1987. Production and scavenging of active oxygen in photosynthesis. In: Kyle, D.J., Osmond, C.B., Arntzen, C.J.(Eds), Photoinhibition. Amsterdam: Elsevier Science Publishers, 227-287.

Bates, H.S., Waldren, R.P., Treare, I.D.,1973. Rapid estimation of free proline for water stress determination. Plant and Soil 39, 205-208.

Bray, H.G., Thorpe, W.V., 1954. Analysis of phenolic compounds of interest in metabolism. Methods of Biochemical Analysis 1, 27-52.

Chakraborty, U., Pradhan, B., 2011. Drought stress-induced oxidative stress and antioxidative responses in four wheat (*Triticum aestivum* L.) varieties. Archives of Agronomy and Soil Science 58, 617-630.

Chakraborty, U., Dutta, S., Chakraborty, B.N., 2002. Response of tea plants to drought stress. Biologia Plantarum 45, 557-562.

Chakraborty, U., Chakraborty, B.N., Kapoor, M., 1993 Changes in the levels of peroxidase and phenyl alanine ammonia lyase in *Brassica napus* cultivars showing variable resistance to *Leptosphaeria maculans*. Folia Microbiologica 38, 491-496.

Chance, B., Machly, A.C., 1955. Assay of catalases and peroxidases. Methods in Enzymology 2, 764-775.

Dhanda, S.S., Sethi, G.S., Behl, R.K., 2004. Indices of drought tolerance in wheat genotypes at early stages of plant growth. Journal of Agronomy and Crop Science 190, 6-12.

Dhindsa, R.S., Dhindsa, P.L., Thrope, T.A., 1981. Leaf senescence: correlated with increased levels of superoxide dismutase and catalase. Journal of Experimental Biology 32, 93-101.

Harborne, J.B., 1973. Phytochemical methods. Chapman and Hall, London Toppan Company Limited, Tokyo Japan.

Heath, R.L., Packer, L., 1968. Photoperoxidation in isolated chloroplasts I: Kinetics and stoichiometry of fatty acid peroxidation. Archives of Biochemistry and Biophysics 125, 189-198.

Jaleel, C.A., 2009. Non-enzymatic antioxidant changes in *Withania somnifera* with varying drought stress levels. American Eurasian Journal of Scientific Research 4, 64-67.

Jena, S., Choudhuri, M.A., 1981. Glycolate metabolism of three submerged aquatic angiosperms during aging. Aquatic Botany 12, 345-354.

Lawlor, D.W., Cornic, G., 2002. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell and Environment 25, 275-294.

Lee, D.H., Lee, C.B., 2000. Chilling stress-induced changes of antioxidant enzymes in the leaves of cucumber in gel enzyme activity assays. Plant Science 159, 75-85.

Leinhos, V., Bergmann, H., 1995. Changes in the yield, lignin content and protein patterns of barley (*Hordeum vulgare* cv. Alexis) induced by drought stress. Angewandte Botanik 69, 206-210.

Lichtenthaler, K., 1987. Chlorophylls and carotenoids pigments of photosynthetic biomembranes. Methods in Enzymology 148, 350-382.

Lowry, O.H., Rosebrough, N.J., Fair, A.L., Randall, R.J., 1951. Protein measurement with folin phenol reagent. Journal of Biological Chemistry 193, 265-275.

Mahadevan, A., Sridhar, R., 1982. Methods of physiological plant pathology 2nd Edn. Sivakami. Publ., India.

Mittler, R., 2002. Oxidative stress, antioxidants and stress tolerance. Trends in Plant Science 7, 405-410.

Mukherjee, S.P., Choudhuri, M.A., 1983. Implications of water stress induced changes in the levels of endogenous ascorbic acid and H_2O_2 in *Vigna* seedlings. Physiologia Plantarum 58, 166-170.

Plummer, D., 1978. An introduction to plant biochemistry. Tata Mc Graw Hill Publications, New Delhi, 362.

Premchandra, G.S., Saneoka, H., Ogata, S., 1990. Cell membrane stability, an indicator of drought tolerance as affected by applied nitrogen in soybean. Journal of Agricultural Science Cambridge 115, 63-66.

Sairam, R.K., 1994. Effect of moisture stress on physiological activities of two contrasting wheat genotypes. Indian Journal of Experimental Biology 32, 594-597.

Tatar, O., Gevrek, M.N., 2008. Influence of water stress on proline accumulation, lipid peroxidation and water content of wheat. Asian Journal of Plant Sciences 7, 409-412.

Vendruscolo, A.C.G., Schuster, I., Pileggi, M., Scapim, C.A., Molinari, H.B.C., Marur, C.J., Vieira, L.G.C., 2007. Stress-induced synthesis of proline confers tolerance to water deficit in transgenic wheat. Journal of Plant Physiology 164, 1367-1376.

Zhu, J.K., 2002. Salt and drought stress signal transduction in plants. Annual Review of Plant Biology 53, 243-273.