The Role of Abscisic Acid in the Response of Two Different Wheat Varieties to Water Deficit

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The changes in plant growth, transpiration rate, photosynthetic activity, plant pigments, electrolyte leakage, H_2O_2 content, lipid peroxidation, catalase activity and endogenous content of abscisic acid (ABA) were followed in the leaves of two wheat varieties (sakha 93 and 94) during drought stress and subsequent rehydration. Drought stress caused several inhibitory changes in the growth of both wheat varieties, particularly in sakha 94. Exogenous ABA treatment improved the growth of sakha 93 plants as indicated by a higher relative water content, transpiration rate and lower electrolyte leakage and also enhanced the growth during the recovery period. Such improvement may be the result of the induction of enzymatic (catalase) and non-enzymatic (carotenoid) systems. ABA treatment did not ameliorate the negative effect of drought on the growth of sakha 94.

Key words: Abscisic Acid, Relative Water Content, Drought Stress

Introduction

Drought is one of the most significant factors among abiotic stresses that limit plant performance, growth and productivity. It induces many physiological, biochemical and molecular responses on plants, such as stomatal closure and reduced transpiration rates, a decrease in water potential and relative water content (RWC) as well as in net photosynthetic CO_2 fixation. Drought also induces the degradation of plasma membranes and high lipid peroxidation (Bajjii *et al.*, 2001; Liu and Baird, 2003; Molnár *et al.*, 2004; Niedzwiedz-Siegien *et al.*, 2004). Moreover, when plants are subjected to various abiotic stresses such as drought, a variety of toxic reactive oxygen species (ROS) such as superoxide radicals ($O_2^{\bullet}$) and hydrogen peroxide (H_2O_2) are noted (Rubio *et al.*, 2002; Jung, 2004). Plants have evolved a series of non-enzymatic (such as ascorbate, α-tocopherol, carotenoids, glutathione) and enzymatic antioxidant systems (such as superoxide dismutase and catalase) to cope with drought stress and to avoid photooxidative damage (Jung, 2004). Ünyayar and Çekiç (2005) suggested that the activities of enzymes of the antioxidant system in plants under stress are usually regarded as an indicator of the tolerance of genotypes to stress conditions.

Since drought stress affects many metabolic pathways, membrane structure, *etc.*, it is not surprising that hormone contents can be also changed by drought stress. This is very important because plant hormones are considered as main signals in root-to-shoot communication and *vice versa* (Naqvi, 1994). Abscisic acid (ABA) is a phytohormone that is involved in many physiological and developmental processes such as transpiration, germination, dormancy and also in the adaptation of plants to various environmental stresses. It has been implicated as a key component in water deficit-induced responses including those triggered by drought, salinity, and low temperature (Pospíšilová *et al.*, 2005). ABA appears to mediate physiological processes in response to osmotic stress. Several studies have reported that the level of endogenous ABA increases in many plants including wheat (Mustafina *et al.*, 1998), tomato (Makela *et al.*, 2003; Thompson *et al.*, 2004), and French bean and tobacco (Pospíšilová *et al.*, 2005) when subjected to osmotic stress. Furthermore, Jiang and Zhang (2002) working on maize leaves documented that, with an increase of the ABA content, the production of ROS and the activities of several antioxidant enzymes – induced by drought stress – were increased.

The present study was undertaken to assess the effects of ABA on some growth parameters, PSII activity, membrane integrity, lipid peroxidation and catalase activity of two wheat varieties, sakha 93 and sakha 94, grown under drought stress.

Materials and Methods

Plant growth, drought and ABA treatments

The grains of two wheat (*Triticum aestivum*) varieties, sakha 93 and sakha 94, were obtained from the Agricultural Research Center, Giza, Egypt. After surface-sterilization with 70% ethanol for 2.5 min the grains were rinsed with distilled water, soaked for 24 h at 25 °C in aerated water and then transferred to weighed plastic pots filled with acid-washed quartz sand.

For drought treatment, two sets of pots were maintained under 70% water holding capacity (WHC) (mild stress) and 30% WHC (severe stress). Drought treatments were imposed from the beginning of the experiment by weighing the pots daily and maintaining them at the desired soil moisture content. For the control treatment (well watered plants) one set of pots was kept at 90% WHC. The pots were placed under natural environmental conditions [approx. (20/15 ± 2) °C day/night temperature and 10/14 h light/dark periods].

ABA (Sigma) treatment was applied on 21-d-old wheat seedlings. 10 ml of 50 or 100 μM ABA solution were applied 3 times at 2-day intervals by spraying the leaves of stressed (30 and 70% WHC) and unstressed plants (90% WHC). Control untreated plants were not sprayed with ABA. 1 d after the last ABA application the seedlings were collected from all treated and untreated plants for fresh and dry biomass determination and chemical analyses. Three pot samples of drought-stressed plants (both sprayed and unsprayed) were rewatered to saturation and left for recovery for 24 h, after which the seedlings were harvested for analyses.

Measurements of physiological parameters

The transpiration rate was estimated as described by Bozuck (1975) and calculated as "g water plant^{-1} d^{-1}". To prevent evaporation from the soil surface, the pots were wrapped in polyethylene bags. Leaf relative water content (RWC) was determined as described by Silveira *et al.* (2003) based on the following equation:

$$\mathrm{RWC} = \{(\mathrm{FW} - \mathrm{DW})/(\mathrm{TW} - \mathrm{DW})\} \cdot 100,$$

where FW is the leaf fresh mass, DW is the dry mass of leaves after drying at 80 °C for 48 h, and TW is the turgid weight of leaves (after soaking in water for 4 h at room temperature) under a photon flux density of 40 μmol m^{-2} s^{-1}. The electrolyte leakage (EL) was measured according to Nayyar *et al.* (2005); leaf samples were washed with deionized water to remove surface-adhered electrolytes, then placed in closed vials containing 20 ml of deionized water and incubated at 25 °C on a rotary shaker for 24 h, before which the electrical conductivity of the solution (L_1) was determined. The leaf samples were then autoclaved at 120 °C for 20 min, and the final electrical conductivity (L_2) was obtained in equilibrium at 25 °C. The electrolyte leakage is defined as:

$$\mathrm{EL}\ (\%) = (L_1/L_2) \cdot 100.$$

The photosynthetic pigments were determined after grinding the leaf samples with acetone following the method described by Metzner *et al.* (1965). The chloroplasts were isolated as described by Osman and El-Shintinawy (1988). The photosynthetic activity, PSII, of both varieties was measured according to Biswall and Mohanty (1976) using the isolated thylakoids. The hydrogen peroxide content was determined according to the method of Velikova *et al.* (2000).

Lipid peroxidation was monitored by spectrophotometric determination of malondialdhyde (MDA) using thiobarbituric acid (TBA) as described in Valentovič *et al.* (2006). Catalase activity (E.C. 1.11.1.6) was determined according to Rios-Gonzalez *et al.* (2002) where the decomposition of H_2O_2 was followed at 240 nm (1 EU = 1 μmol H_2O_2 decomposed in 1 min).

The ABA content in the leaves (of severe stressed, control and rewatered plants, both sprayed and unsprayed) was estimated by HPLC. Weighed leaves were thoroughly extracted in acetone containing 0.1% butylhydroxytoluene (Sharma *et al.*, 2002). The extract was centrifuged at 5000 × *g* for 5 min at 4 °C. The supernatant was filtered through a 30 μm syringe filter, and 10 μl of the filtrate were used for HPLC analysis. The separation and quantitative estimation were carried out using a HPLC system (Perkin Elmer series 200 LC and UV/VIS detector 200 LC, USA) equipped with a 5 μm column (Spheri-5 RP-18, 220 × 4.6 mm, Brownlee). The solvent used was acetonitrile/water (26:74) run isocratically. The detector was set at 440 nm for the integration of peak areas after calibration with the external standard ABA.

Results and Discussion

Changes in transpiration rate and growth criteria of wheat plants

Increasing drought stress had a significant inhibitory effect on fresh and dry biomass as well as

shoot height of the two wheat varieties, particularly in sakha 94. Under severe drought stress, spraying sakha 93 plants with 50 or 100 μM ABA resulted in a significant increase in fresh and dry biomass and shoot height compared with the unsprayed controls. Conversely, spraying the variety sakha 94 with ABA significantly decreased the growth. Rewatering significantly increased the fresh and dry biomass of water-stressed sakha 93 plants whereas in sakha 94 only the fresh biomass was significantly increased (Table I). The transpiration rate was significantly decreased in the two wheat varieties with increasing water stress. Under severe water stress, ABA treatment resulted in a marked improvement of the transpiration rate only with sakha 93.

The development of water stress decreased the leaf RWC of both wheat varieties relative to the well watered control plants (Table II). Application of exogenous ABA significantly increased the RWC in sakha 93 plants. For example, at 30% WHC, the leaf RWC of 50 and 100 μM ABA-sprayed sakha 93 plants was 39.2 and 28.8%, respectively, compared to 21.0% in the unsprayed control plants. The corresponding values for sakha 94 plants were 15.4, 12.6 and 16.9%. A higher RWC after pretreatment with ABA has been recorded for other plants such as tall fescue (Jiang and Huang, 2002) and tobacco (Pospíšilová *et al.*, 2005).

Electrolyte leakage (EL) in both wheat varieties significantly increased under mild and severe water stress (Table II). Foliar spraying of sakha 93 plants with 50 and 100 μM ABA decreased the percentage of EL in severe stressed plants but resulted in an increased EL in sakha 94. Rewatering the plants slightly decreased the percentage of EL in the two wheat varieties, and treatment with ABA enhanced the recovery of both wheat varieties but the effect was more obvious in sakha 93.

Changes in photosynthetic pigments and PSII of wheat plants

Successive progress in drought stress of both wheat varieties resulted in a significant decrease in chlorophyll, chl a and b, and a significant increase in carotenoids (car) contents (Table III). Under severe water stress, ABA treatment resulted in a significant decrease in photosynthetic pigments contents of sakha 94 plants, whereas in

Table I. Effect of drought, exogenous ABA and rewatering on fresh and dry biomass, shoot height and transpiration rate of two wheat varieties, sakha 93 and 94. Values are the means of 3 independent replicates. WHC, water holding capacity; 90% WHC, well watered; 70% WHC, mild stress; 30% WHC, severe stress.

ABA treatment	WHC (%)	Fresh biomass [g/plant]		Dry biomass [g/plant]		Shoot height [mm]		Transpiration rate [g H_2O/plant/d]	
		Sakha 93	Sakha 94	Sakha 93	Sakha 94	Sakha 93	Sakha 94	Sakha 93	Sakha 94
Control – ABA	90	0.358^{a}	0.344^{a}	0.039^{ab}	0.032^{a}	26.7^{a}	21.9	2.49^{a}	2.34^{a}
	70	0.302^{b}	0.194^{b}	0.034^{bc}	0.028^{bc}	19.1^{b}	16.8^{bc}	2.19^{c}	1.89^{b}
	30	0.144^{e}	0.086^{e}	0.012^{e}	0.010^{e}	8.5^{d}	7.9^{ef}	1.05^{e}	0.48^{d}
+ 50 μM ABA	90	0.352^{a}	0.336^{a}	0.040^{a}	0.032^{a}	25.5^{a}	20.7^{a}	2.45^{b}	2.56^{a}
	70	0.312^{b}	0.150^{cd}	0.040^{a}	0.024^{c}	20.9^{b}	14.9^{cd}	2.42^{b}	1.41^{bc}
	30	0.201^{d}	0.082^{e}	0.018^{d}	0.090^{fg}	12.6^{c}	4.6^{f}	1.76^{f}	0.41^{d}
+ 100 μM ABA	90	0.366^{a}	0.236^{a}	0.037^{ab}	0.029^{a}	24.5^{a}	18.6^{ab}	2.55^{a}	2.08^{ab}
	70	0.288^{c}	0.121^{d}	0.029^{c}	0.019^{d}	20.1^{b}	10.3^{de}	2.21^{c}	0.84^{c}
	30	0.173^{d}	0.044^{f}	0.015^{de}	0.060^{g}	12.0^{c}	4.7^{f}	1.26^{d}	0.38^{d}
Control rewatered – ABA	90	0.365^{a}	0.364^{a}	0.052^{ab}	0.034^{a}	27.4^{a}	22.3^{a}	2.64^{a}	2.40^{a}
	70	0.322^{b}	0.207^{d}	0.046^{c}	0.029^{b}	21.8^{e}	16.7^{b}	2.45^{a}	2.03^{c}
	30	0.160^{d}	0.110^{g}	0.016^{d}	0.010^{d}	9.7^{g}	8.1^{d}	1.64^{c}	0.45^{f}
Rewatered + 50 μM ABA	90	0.372^{a}	0.348^{b}	0.054^{a}	0.034^{a}	26.0^{cb}	22.4^{a}	2.66^{a}	2.39^{ab}
	70	0.332^{b}	0.266^{c}	0.043^{a}	0.024^{c}	22.5^{de}	16.1^{b}	2.59^{a}	1.86^{d}
	30	0.246^{c}	0.129^{f}	0.025^{d}	0.010^{d}	14.9^{f}	4.7^{e}	2.14^{b}	0.38^{f}
Rewatered + 100 μM ABA	90	0.360^{a}	0.259^{c}	0.053^{a}	0.030^{ab}	25.8^{b}	17.9^{b}	2.68^{a}	2.14^{bc}
	70	0.322^{b}	0.158^{e}	0.048^{bc}	0.022^{c}	25.0^{cd}	10.5^{cd}	2.39^{a}	0.95^{e}
	30	0.181^{d}	0.126^{fg}	0.021^{d}	0.070^{d}	14.7^{f}	4.8^{e}	2.05^{b}	0.37^{f}

LSD, means indexed by the same superscript are not significantly different at $P \geq 0.05$.

ABA treatment	WHC (%)	RWC (%)		EL (%)	
		Sakha 93	Sakha 94	Sakha 93	Sakha 94
Control – ABA	90	63.7^{b}	52.8^{a}	5.5^{d}	4.7^{e}
	70	46.4^{c}	39.4^{d}	15.3^{b}	23.4^{d}
	30	21.0^{e}	16.9^{fg}	35.9^{a}	46.7^{b}
+ 50 μM ABA	90	71.0^{a}	51.1^{ab}	5.9^{d}	5.7^{e}
	70	69.5^{b}	41.6^{c}	14.1^{b}	30.1^{c}
	30	39.2^{cd}	15.4^{gh}	23.5^{d}	57.2^{b}
+ 100 μM ABA	90	65.9^{a}	50.9^{b}	5.9^{d}	5.7^{e}
	70	69.8^{b}	22.8^{e}	10.2^{c}	34.5^{c}
	30	28.8^{d}	12.6^{b}	21.3^{a}	78.6^{a}
Control rewatered – ABA	90	69.9^{a}	61.8^{a}	5.3^{e}	4.6^{e}
	70	58.7^{de}	59.8^{b}	13.3^{b}	18.2^{d}
	30	49.4^{e}	17.1^{g}	28.5^{a}	45.8^{c}
Rewatered + 50 μM ABA	90	90.1^{a}	62.4^{a}	5.9^{e}	4.8^{e}
	70	85.8^{b}	51.4^{d}	10.3^{cde}	19.4^{d}
	30	69.7^{c}	15.3^{e}	11.3^{c}	50.3^{b}
Rewatered + 100 μM ABA	90	98.7^{a}	56.3^{c}	5.9^{e}	5.1^{c}
	70	88.2^{b}	25.5^{f}	8.2^{de}	24.0^{d}
	30	59.9^{d}	13.0^{h}	19.4^{b}	69.4^{a}

Table II. Effect of exogenous ABA (50, 100 μM) on relative water content (RWC) and electrolyte leakage (EL) during the development of water stress and subsequent rewatering of two wheat varieties, sakha 93 and sakha 94. Values are means of 3 independent replicates. WHC, water holding capacity; 90% WHC, well watered; 70% WHC, mild stress; 30% WHC, severe stress.

LSD, means indexed by the same superscript are not significantly different at $P \geq 0.05$.

Table III. Changes in photosynthetic pigments (mg/g dry mass) and PSII activity (μmol reduced DCPIP/μg chl/mg FM) in the leaves of wheat seedlings (sakha 93 and 94) in response to drought, exogenous ABA and rewatering. Values are the means of 3 independent replicates. Chl, chlorophyll; car, carotenoids; WHC, water holding capacity; 90% WHC, well watered; 70% WHC, mild stress; 30% WHC, severe stress.

ABA treatment	WHC (%)	Sakha 93					Sakha 94				
		Chl a	Chl b	Car	Car/ chl(a+b)	PSII activity	Chl a	Chl b	Car	Car/ chl(a+b)	PSII activity
Control – ABA	90	35.64^{a}	20.43^{a}	15.54^{d}	0.28	0.417^{a}	34.99^{a}	20.66^{a}	12.39^{f}	0.22	0.430^{a}
	70	34.51^{a}	20.89^{a}	25.88^{b}	0.47	0.340^{b}	28.43^{a}	20.17^{a}	28.32^{e}	0.58	0.307^{b}
	30	24.63^{c}	19.25^{bc}	40.45^{a}	0.92	0.105^{d}	17.84^{d}	15.62^{b}	36.31^{cd}	1.09	0.052^{f}
+ 50 μM ABA	90	36.02^{a}	20.86^{a}	15.92^{d}	0.28	0.420^{a}	33.65^{a}	19.30^{a}	17.94^{f}	0.34	0.307^{b}
	70	31.47^{b}	20.35^{a}	19.74^{c}	0.38	0.364^{b}	26.24^{b}	21.54^{a}	33.11^{cde}	0.69	0.280^{c}
	30	24.89^{c}	18.92^{bc}	26.69^{b}	0.61	0.161^{c}	14.24^{de}	12.66^{bc}	48.23^{ab}	1.79	0.023^{f}
+ 100 μM ABA	90	34.91^{a}	22.61^{a}	15.17^{d}	0.27	0.393^{ab}	28.87^{ab}	19.70^{a}	29.91^{de}	0.62	0.168^{d}
	70	30.08^{b}	20.33^{ab}	19.62^{c}	0.39	0.338^{b}	20.64^{c}	20.93^{a}	41.13^{bc}	0.99	0.104^{c}
	30	24.79^{c}	17.02^{c}	27.49^{b}	0.66	0.188^{c}	10.17^{e}	9.68^{c}	52.14^{a}	2.63	0.020^{f}
Control rewatered – ABA	90	36.66^{a}	20.48^{a}	15.41^{cd}	0.27	0.499^{ab}	35.22^{a}	21.65^{a}	13.09^{f}	0.23	0.443^{a}
	70	33.45^{b}	21.69^{a}	14.67^{d}	0.28	0.461^{c}	30.78^{bc}	22.72^{a}	21.08^{d}	0.41	0.392^{b}
	30	23.72^{d}	20.05^{a}	20.22^{ab}	0.46	0.145^{g}	17.66^{ef}	16.65^{c}	26.02^{cd}	0.76	0.061^{f}
Rewatered + 50 μM ABA	90	35.56^{a}	22.15^{a}	14.88^{d}	0.26	0.507^{a}	34.19^{ab}	19.72^{bc}	14.99^{ef}	0.28	0.392^{b}
	70	31.72^{bc}	20.38^{a}	14.43^{d}	0.28	0.485^{b}	25.88^{d}	21.21^{ab}	31.08^{bc}	0.66	0.328^{c}
	30	25.70^{d}	15.24^{b}	17.75^{b}	0.46	0.258^{e}	14.85^{fg}	12.08^{d}	47.77^{a}	1.77	0.091^{f}
Rewatered + 100 μM ABA	90	34.56^{ab}	22.23^{a}	14.45$^{•}$	0.25	0.463^{c}	28.09^{cd}	22.55^{a}	21.43^{de}	0.42	0.182^{d}
	70	31.21^{c}	20.14^{a}	15.07^{d}	0.29	0.370^{d}	20.41^{e}	20.24^{ab}	37.82^{b}	0.93	0.118^{e}
	30	24.32^{d}	17.95^{b}	21.11^{a}	0.50	0.228^{f}	10.50^{g}	9.19^{d}	50.11^{a}	2.54	0.062^{f}

LSD, means indexed by the same superscript are not significantly different at $P \geq 0.05$.

sakha 93 there was almost no change. Furthermore, the car/chl a+b ratios were markedly increased in both wheat varieties with decreasing soil moisture, and spraying the plants with ABA resulted in a decrease in this ratio in sakha 93 and an increase in sakha 94 plants. Rehydration decreased the car/chl a+b ratio particularly in sakha 93.

PSII of both wheat varieties decreased under drought stress compared to control well watered plants (Table III). Spraying the leaves with ABA resulted in a significant increase in PSII activity in severely stressed sakha 93 plants; the opposite trend was recorded for sakha 94 plants. Rewatering significantly increased the PSII activity only in sakha 93; the increase in sakha 94 was insignificant.

Changes in lipid peroxidation, H_2O_2 content, catalase activity and ABA content of wheat plants

Increasing drought stress led to a significant increase in lipid peroxidation, H_2O_2 content and catalase activity of the two wheat varieties (Fig. 1). Under severe water stress ABA treatment resulted in a significant decrease in the MDA content of both wheat varieties. Rehydration of both wheat varieties decreased the MDA content most

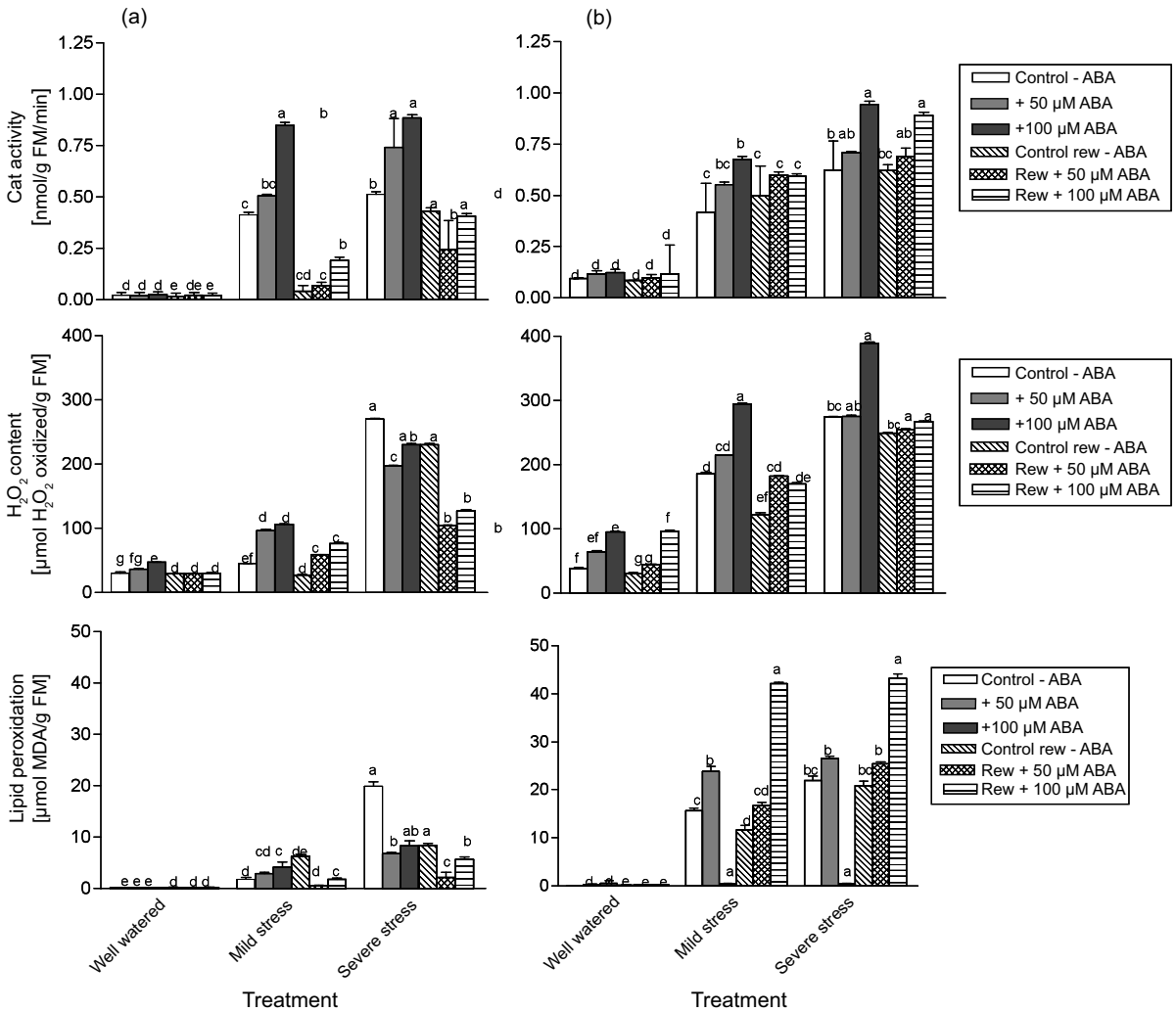

Fig. 1. Effect of exogenous ABA (50, 100 μM) on catalase (cat) activity, H_2O_2 content and lipid peroxidation during development of drought stress and subsequent rewatering of two wheat varieties, (a) sakha 93 and (b) sakha 94. Values are means ± SE (n = 3). 90% WHC, well watered; 70% WHC, mild stress; 30% WHC, severe stress.

notably in sakha 93 (Fig. 1). Foliar spray with ABA enhanced the recovery of sakha 93 but has an inhibitory effect on the membrane structure of sakha 94 as it is evident by the increase in its MDA content.

Spraying with 50 and 100 μM ABA resulted in a significant increase in the catalase activity of both wheat varieties under severe water stress. This was accompanied with a significant decrease of the H_2O_2 content in sakha 93 and a significant increase in sakha 94. Under severe water stress, spraying sakha 94 plants with 100 μM ABA increased the H_2O_2 content and catalase activity by 1.4- and 1.5-fold, respectively, compared to the unsprayed controls. Rehydration of wheat plants (treated, untreated) decreased the H_2O_2 content and catalase activity in both wheat varieties.

The endogenous ABA contents increased significantly in the two wheat varieties in response to severe drought stress. Similar results were reported for bean, tobacco and maize plants (Pospíšilová *et al.*, 2005). The endogenous ABA content was markedly increased after ABA pretreatment in both wheat varieties (Table IV) which is in agreement with previous results (Sauter and Hartung 2000; Sauter *et al.*, 2002) showing that ABA can move freely through the plant in both the xylem and the phloem. Under severe water stress, the ABA content was about 2- and 2.5-fold the values in well-watered sakha 93 and sakha 94 plants, respectively, and after spraying the plants with 50 μM ABA they were 2.3- and 3.1-fold.

Table IV. Effect of exogenous ABA (50, 100 μM) on ABA content during the development of drought stress and subsequent rewatering of two wheat varieties, sakha 93 and sakha 94. WHC, water holding capacity; 90% WHC, well watered; 30% WHC, severe stress.

ABA treatment	WHC (%)	ABA [μM]	
		Sakha 93	Sakha 94
Control – ABA	90	0.706	0.842
	30	1.445	2.075
+ 50 μM ABA	90	2.798	2.049
	30	6.519	6.354
+ 100 μM ABA	90	4.770	4.538
	30	8.582	8.263
Control rewatered – ABA	90	0.706	0.842
	30	1.019	1.354
Rewatered + 50 μM ABA	90	0.775	1.914
	30	2.397	5.786
Rewatered + 100 μM ABA	90	0.802	2.377
	30	4.605	8.092

It is well known that drought is the most important stress factor determining plant growth rates and stomata movement. In this investigation, the decrease in the transpiration rate may be related to the induction of stomatal closure under drought condition which affects the growth by reducing the water uptake (Lopez *et al.*, 2002; Jung, 2004) and photosynthesis (Simova-Stoilova *et al.*, 2006) as well as disturbance of plasma membrane integrity (Chaves and Oliveira, 2004). Data concerning leaf RWC and EL revealed that the relative water content and the cell membrane permeability suffer from drought injury. ABA treatment and rehydration enhanced to some extent the drought tolerance in sakha 93, while it did not ameliorate the negative effect of drought on the growth of sakha 94 and visible wilting was observed. These observations suggest that the two wheat varieties are different in their response to ABA. The decrease in photosynthetic pigments (chl a and b) and PSII activity of both wheat varieties in response to drought stress may be related to a damage in membrane disintegration due to oxidative stress (Moran *et al.*, 1994, Alonso *et al.*, 2001) as well as a damage of PSII reaction centres (Asada, 1999). On the other hand, the increase in carotenoids content and car/chl a+b ratio may be considered as an adaptive feature that reduces the possibility of further damage of the photosynthetic apparatus by the formed ROS and controls the energy dissipation in the antenna (Kranner *et al.*, 2002). The photoprotective role of carotenoids in drought stress has previously been reported with *Citrus* species (Kato *et al.*, 2004) and *Arabidopsis thaliana* (Jung, 2004). Data in the present investigation showed also that ABA may have shifted off the inhibitory oxidative effect of drought stress on the photosynthetic machinery of sakha 93, while it enhanced senescence and oxidative damage in sakha 94. It has been documented that ABA treatment results in an increased generation of ROS in maize and broad bean plants (Guan *et al.*, 2000; Zhang *et al.*, 2001) which leads to photooxidative damage and disturbance of the plasma membrane. Several investigators have reported that the H_2O_2 content increases in response to exogenous ABA (Zhang

et al., 2001; Jiang and Zhang, 2002). In the present investigation, the increased H_2O_2 and MDA contents as well as catalase activity in sakha 94 plants during drought stress and after ABA treatment and rehydration may explain the reduction in plant growth as a result of membrane injury and reducted water uptake. The opposite trend observed in sakha 93 indicates that ABA may induce the enzymatic antioxidant system to depress the inhibitory effect of ROS on the plasma membrane and hence improve the growth. Such increased catalase activity in response to drought has previously been reported on *Arabidopsis thaliana* by Jung (2004). In addition, the positive effect of exogenous ABA on the catalase activity was also reported in young maize leaves (Guan *et al.*, 2000) and tomato (Ünyayar and Çekiç, 2005).

In conclusion, drought stress caused several inhibitory changes in the growth of both wheat varieties particularly in sakha 94. Exogenous ABA treatment seemed to improve the growth of sakha 93 plants through induction of enzymatic (catalase) and non-enzymatic (carotenoids) systems and hence protect the plasma membrane integrity and keep water conservation. On the other hand, disruption of plasma membranes and decrease in PSII activity of sakha 94 were greatly enhanced by ABA application. Taken as a whole, this study may indicate that sakha 93 is more tolerant to drought stress than sakha 94 and that sakha 94 is sensitive to both drought and ABA.

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