Effect of Exogenous Polyamines on Some Physiological Characteristic and Carbohydrate Metabolism in Rice (*Oryza sativa* L.) Under Drought Stress

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ABSTRACT

Drought stress is the main environmental problems decreasing growth and metabolic processes of rice. This research aimed to study the effects of exogenous polyamines on some physiological characteristic and carbohydrate metabolism in rice seedlings cv. Khao Dawk Mali 105 (*Oryza sativa* L.) under drought stress. Three polyamines were studied including putrescine, spermidine and spermine. Seedlings were grown for 14 days and foliar sprayed with 300 ml of 10 µM Spd, Spm and Put for 2 days. Irrigation was withheld for 7 days except in control group which was watered daily. The results showed that Spm and Put slightly improved seedling growth under drought stress but was not significantly different. In addition, Spm and Put also increased relative water content and reduced electrolyte leakage. PAs also increased sugar accumulation of plants under stress. These results suggested that PAs can alleviate the effects of drought stress by increasing sugar accumulation in rice.

Keywords: Polyamines, Drought stress, Carbohydrate metabolism

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Introduction

Rice (*Oryza sativa* L.) is an important crop that supports much of the rural population of Thailand. Drought is one of the main important abiotic stress factors inhibiting photosynthesis and decreasing growth and productivity of plant (Zlatev and Lidon, 2012). Photosynthesis inhibition is caused by decreasing internal CO_2 concentration due to stomatal closure. Drought affects not only photosynthetic rate, but also decrease relative water content (RWC), leaf water potential and rate of transpiration (White *et al*., 2000). Reduction of water content disrupts the integrity of plasma membrane, the activity of various cellular enzymes, as well as the function of plant photosynthetic apparatus (Gupta, *et al*., 2013).

Several plants have many mechanisms to survive water deficit, such as tolerance and avoidance of stress (Turner, 1986). Many mechanisms are designed to alleviate the effects of stress such as changes in metabolic processes, increased solute accumulation, changes in physiological characteristics and anatomy (Xu *et al*., 2006). Many studies have shown that plant growth regulators accumulation occurs in plants exposed to drought, which indicates that plant growth regulators plays an important role in drought tolerance. Exogenous application of plant growth regulators has been known to increase plant tolerant toward abiotic stresses. Among the plant growth regulators, polyamines (PAs) were reported to improve the growth rate of rice seedlings under drought stress (Farooq *et al*., 2009a). In recent years, there have been many studies on the exogenous application of PAs for enhanced abiotic tolerance such as salinity but only few have reports the role of PAs in drought stress. PAs, such as spermine, spermidine and putrescine, are known as major and the most common PAs, have a small ubiquitous polycations involved in many physiological processes, including plant growth and development, cell division, embryogenesis, root initiation, floral initiation and senescence (Evans and Malmberg, 1989). However, there are only a few reports on PAs effect on physiological characteristic and carbohydrate metabolism in rice (*Oryza sativa* L.) under drought stress. It has been reported that exogenous application of PAs plays important roles in membrane stability (Zhao and Yang, 2008). Farooq *et al.* (2009a) have studied that the exogenously applied polyamines increase drought tolerance of rice by improving the leaf water status, photosynthesis and membrane properties. The results showed that drought stress reduced rice fresh and dry weights, while the exogenous application of PAs increased net photosynthesis, water use efficiency, leaf water status, production of free proline, anthocyanins and soluble phenolics and improved membrane properties. These results indicated that PAs may be related to drought tolerance. Thus, this study aimed to study effects of polyamines on some physiological characteristics and carbohydrate metabolism in rice (*Oryza sativa* L.) under drought stress.

Objective of the study

The studies aimed to investigate the effects of polyamines on some physiological characteristics and carbohydrate metabolism in rice (*Oryza sativa* L.) under drought stress.

Materials and methods

Plant material and growth conditions: Seeds of rice (*Oryza sativa* L. cv. KDML105) were supplied by Khon Kaen Rice Experimental Stations. Rice seeds were soaked in distilled water for 48 h. Rice seeds were then germinated on moistened filter paper in the dark for 3 days. After germination, seedlings were grown in potted soil in a greenhouse under natural light condition. Two-weeks-old plants were separated into 5 treatments including 1) control, 2) drought, 3) Putrescine (Put), 4) Spermine (Spm) and 5) Spermidine (Spd). For control and drought groups, the seedlings were foliar-sprayed with 300 ml distilled water whereas Put, Spm and Spd groups, the seedlings were foliar-sprayed with 300 ml of 10 µM Put, 10 µM Spm and 10 µM Spd, respectively. All seedlings were sprayed at 11 a.m. for 2 consecutive days. Irrigation was withheld for 7 days except in the control group which was watered daily with distilled water.

Measurement of plants growth: Two seedlings per pot were randomly sampled for measurement of shoot and root lengths after being washed with distilled water. Root and shoot lengths of 2 plants from each treatment were determined. Fresh weights of shoot and root tissues were recorded and then the tissues were oven-dried at 80 °C for 3 days in order to determine dry weight.

Determination of relative water content, electrolyte leakage, score of leaf rolling and chlorophyll contents: Relative water content (RWC) was measured by the method of Turner (1981). Leaves were cut to 0.5 x 0.5 cm. Fresh weight of leaves was determined. Leaves were then soaked in deionized distilled water for 12 h. After that, rehydrated fresh weight was determined and then the tissues were placed in a preheated oven at 80 °C for 3 days to obtain dry weight. RWC were calculated according to the following formula:

(fresh weight – dry weight) / (rehydrated fresh weight - dry weight) × 100

For determination of electrolyte leakage, leaf tissues were soaked in 10 ml distilled water for 24 h. Electrical conductivity was measured before boiling (ECb) by a conductivity meter. Then, the tubes containing the tissues were boiled at 100 °C for 20 min. Electrical conductivity was measured after boiling (ECa). Electrolyte leakage was measured by the method of Baninasab and Ghobadi (2011) using the following formula.

((ECb) / (ECa)) / × 100

For determination of leaf rolling, the plants were scored for leaf rolling at 11 a.m. for 2 times after stress. Two leaves per pot were scored using 0-9 scale of standard evaluation system for rice. Score of leaf rolling was measured by the method of IRRI (1996) using the following standard evaluation;

0 leaves healthy, 1 leaves starts to fold, 3 leaves folding (deep V- shaped), 5 leaves fully cupped (U- shaped), 7 leaves margins touching (O-shaped) and 9 leaves tightly rolled.

Leaf chlorophyll contents were measured by Arnon (1949) method. Ten milliliter of 80% acetone were added in the tube containing approximately 50 mg of leaf tissue and then placed in the dark at room temperature for 48 h. The extract was determined by spectrophotometer at 645 nm and 663 nm using 80% acetone as blank.

Measurement of carbohydrate metabolism:

Leaf sample was randomly selected from control and stressed plants. Soluble sugar was extracted with 3 ml of 80% (v/v) ethanol (Dubois *et al*., 1956). The sucrose and fructose contents were determined by resorcinol – HCl method. Five hundred µl of 0.2 N NaOH was added to leaf sugar extract and boiled at 100°C for 10 min to destroy fructose and used for sucrose determination. All tubes were then added with 0.25 ml 1% resorcinol and 0.75 ml 30% HCl. The tubes were boiled at 80°C for 10 min and cooled down. The absorbance was measured at 520 nm with a spectrophotometer. Fructose concentration was calculated by subtracting sucrose from sucrose + fructose (Robbins and Pharr 1987). The glucose content was determined by hexokinase, glucose-6-phosphate dehydrogenase (G6PDH) (Madore 1990). Twenty µl of sugar extract was put into a test tube containing 50 mM Tris-HCl, 500 mM $MgCl_2$, 100 mM NAD, 1 U HK and 0.2 U G6PDH, the tubes were then mixed by shaking for 30 min. The absorbance was measured at 360 nm. Starch content was measured by determining glucose hydrolyzed from hexokinase and glucose-6-phosphate dehydrogenase reaction. Known concentrations of glucose were used as a standard (Madore, 1990).

Enzyme extraction and assay: One gram tissue was ground using motar and pestle in 4 mL grinding buffer containing 50 mM HEPES, 10 mM EDTA, 1% polyethyleneglycol-20, 0.25% BSA and 5 mM dithiothreitol, pH 7.5. The supernatant was partially purified on Sephadex G25 column equilibrated with grinding buffer. The amount of protein in the enzyme extract was determined by Bradford method (Bradford, 1976). SPS activity was determined by measuring sucrose-6-phosphate produced from substrates, UDP-glucose and fructose-6-phosphate. (Robbins and Pharr, 1987). Invertase activities were determined under acidic (pH 4.0) and alkaline (pH 7.6) conditions.

Data analysis: Data was analyzed using SPSS version 16.0 and means of each treatment were compared using one-way ANOVA followed by Duncan's multiple range test at 0.05 level of significance.

Result

Physiological characteristics: Drought stress significantly decreased seedling growth. Root fresh and dry weight, shoot fresh and dry weight, root and length were reduced by 76.4, 59.6, 69.9, 35.5, 11.6 and 17.3% respectively, when compared to the control plants. However, application of Put increased root fresh and dry weight in the stressed plants by 19.4% and 12.8% respectively, compared to the untreated plants. In addition, the exogenous application of Spm and Spd significantly increased shoot fresh weight in the stressed plants by 51.7% and 16.4% respectively, compared to the untreated plants (Table 1).

Relative water content, electrolyte leakage, score of leaf rolling and chlorophyll contents: Drought stresses caused significant reduction in relative water content. Relative water content was reduced from 82.1% in the control to 70.2% in the droughted plants. Foliar application of Spm and Put slightly increased relative water content and the values were higher than those of the untreated plants (Fig. 1a). Electrolyte leakage in the leave was increased by drought stress. Electrolyte leakage increased from 6.63% in the control plants to 16.16% in the droughted plants. However, exogenous application of Put and Spm decreased electrolyte leakage in the droughted plants to 8.02, 8.5 and 15.0%, respectively. In addition, drought stress significantly increased score of leaf rolling compare to the droughted plants. Foliar spray with PAs decreased leaf rolling. In addition, drought stress significantly decreased chlorophyll *a*, chlorophyll *b* and total chlorophyll contents. Chlorophyll *a*, *b* and total chlorophyll were reduced from 8.75, 2.82 and 16.61 mg g^{-1} FW in the control plants, respectively. Exogenous application of Spm shown significantly increases in chlorophyll *a*, *b* and total chlorophyll (Fig.1c-1e).

Table1 Effect of exogenous application of PAs on physiological characteristics of rice seedling under drought stress

Treatments	root fresh weight (g plant $^{-1}$)	root dry weight (g plant $^{-1}$)	shoot fresh weight (g plant $^{-1}$)	shoot dry weight (g plant $^{-1}$)	root length (cm)	shoot length (cm)
Control	0.547 ± 0.090 ^{b}	0.075 ± 0.008 ^{b}	1.518 ± 0.060 ^{c}	0.344 ± 0.040 ^{b}	21.775 ± 1.506 ^{b}	59.025 ± 1.118 ^{b}
Drought	0.129 ± 0.009 ^{a}	0.047 ± 0.001 ^{a}	0.456 ± 0.003 ^{a}	0.222 ± 0.027 ^{a}	19.250 ± 0.661 ^{ab}	48.833 ± 0.666 ^{a}
Put + drought	0.154 ± 0.027 ^{a}	0.053 ± 0.007 ^{a}	0.531 ± 0.040 ^{ab}	0.215 ± 0.029 ^{a}	16.800 ± 1.602 ^{a}	47.950 ± 1.840 ^{a}
Spm + drought	0.129 ± 0.018 ^{a}	0.045 ± 0.005 ^{a}	0.692 ± 0.040 ^{b}	0.206 ± 0.001 ^{a}	17.625 ± 0.240 ^{ab}	47.175 ± 1.417 ^{a}
Spd + drought	0.106 ± 0.017 ^{a}	0.040 ± 0.006 ^{a}	0.530 ± 0.078 ^{b}	0.184 ± 0.017 ^{a}	16.250 ± 1.984 ^{a}	46.950 ± 0.904 ^{a}

The results are the mean ± SE (n = 4). The Duncan's multiple range was tested at $P < 0.05$ level of significance.

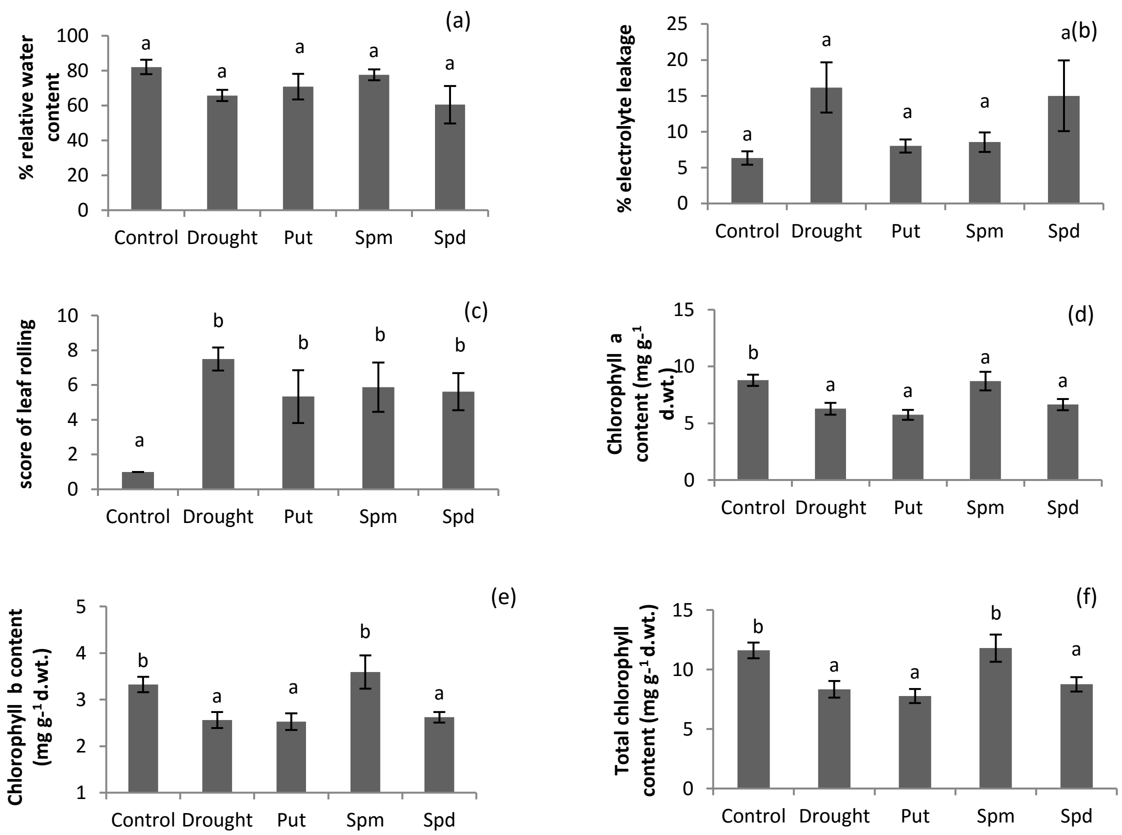
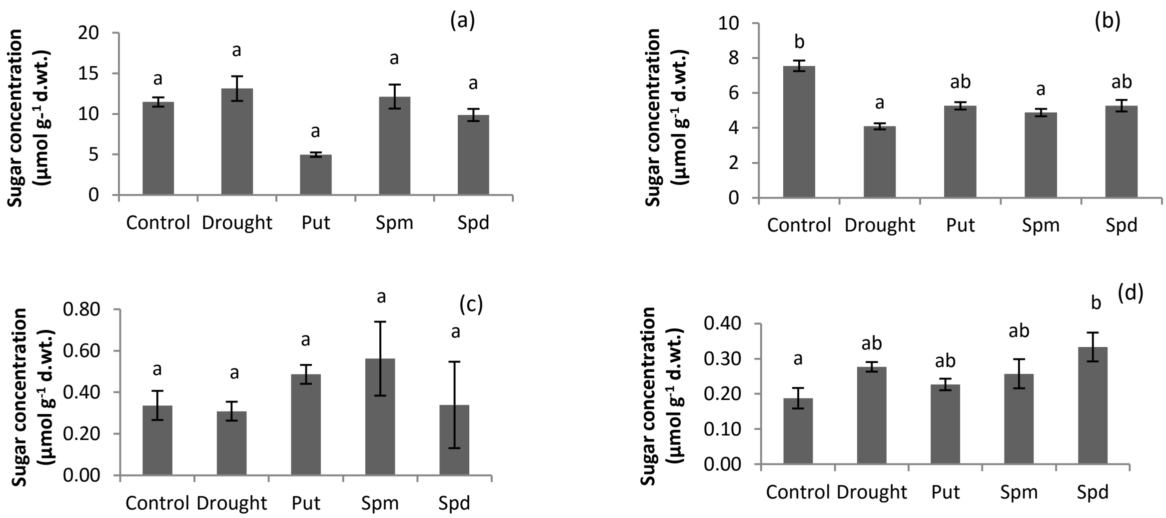


Fig. 1 Effect of exogenous application of PAs on (a) % relative water content, (b) % electrolyte leakage, (c) score of leaf rolling, (d) chlorophyll a, (e) chlorophyll b and (f) total chlorophyll in mature leave under drought stress. The data represent the mean ± SE (n=4). The Duncan's multiple range was tested at $P < 0.05$ level of significance. (Cont.)

Carbohydrate metabolism: Drought stress increased total soluble sugar content and glucose content in leaves of the stressed plants (Fig. 2a, 2b). Total sugar and glucose were increased from 11.472 and 0.188 µmol g^{-1} d.wt in the control plants to 13.125 and 0.277 µmol g^{-1} d.wt. in the droughted plants (Fig. 2a,2b). Exogenous application of PAs had no effects on total soluble sugar content in leaf under drought stress (Fig. 2a). In contrast, exogenous application of Spd increased glucose in the droughted plants to 0.333 µmole g^{-1} d.wt. compared to 0.277 µmole g^{-1} d.wt. in the untreated plants (Fig. 2b). Drought stress also caused reduction in sucrose and fructose contents (Fig. 2c, 2d). Application of exogenous PAs and Spm increased sucrose and fructose compared to the untreated plants (Fig. 2c, 2d). In contrast, foliar spray with PAs had no increase in starch accumulation compared to the untreated plants (Fig. 2e).

Enzyme activities: Accumulation of sugars was also reflected by increasing SPS activities under drought stress. Exogenous application of Put and Spd also increased protein in the stressed plants (Fig. 3a). SPS activities increase from 13.23 µmole/mg protein/h. in the control plants to 14.02 µmole/mg protein/h. in the droughted plants. Exogenous application of Spm and Spd also increased SPS activities to 16.02 and 20.16 µmole/mg protein/h., respectively (Fig. 3b). In addition, application of Spm, Spd and Put also increase alkaline invertase activities to 17.079, 15.519 and 11.136 µmole/mg protein/h., respectively (Fig. 3c), whereas application exogenous of PAs had no significant effect on acid invertase in the stressed plants (Fig.3d).



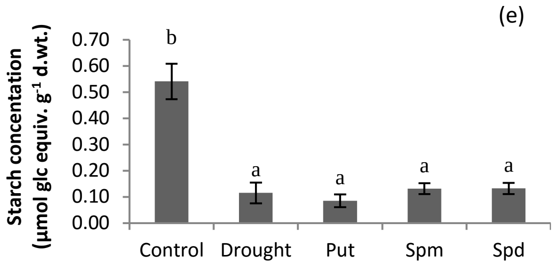


Fig. 2 Effect of exogenous application of PAs on (a) total sugar content, (b) glucose content, (c) sucrose content, (d) fructose content and (e) starch content in mature leave under drought stress. The data represent the mean ± SE (n=4). The Duncan's multiple range was tested at P < 0.05 level of significance. (Cont.)

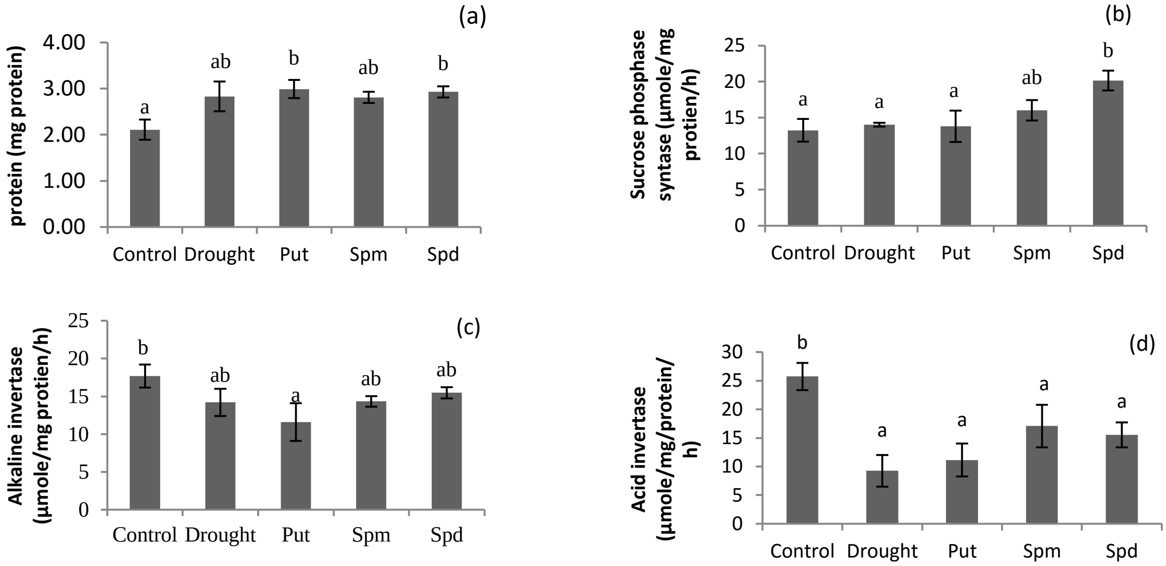


Fig. 3 Effect of exogenous application of PAs on (a) protein content, (b) SPS activities, (c) alkaline invertase and (d) acid invertase in mature leave under drought stress. The data represent the mean ± SE (n=4). The Duncan's multiple range was tested at P < 0.05 level of significance.

Discussion and Conclusion

Drought stress is major abiotic stress that affects growth and productivity of crop plants (Radhakrishnan and Lee, 2013). The present study showed that drought stress caused reduction in plants growth. Exogenous application of PAs had been reported to induce various processes including stress response in *Arabidopsis* (Tun, *et al*., 2006). Application of PAs induces stomatal closure by increasing signal molecule under stress (Pottosin and Shabala, 2014; Moschou *et al*., 2008). Stomatal closure leads to limiting photosynthesis CO_2 assimilation under stress (Liu et al., 2005 ; Pattanagul, 2011).

The relative water content in leaf was reduced under drought stress. Exogenous application of polyamines improved drought tolerance of rice by improving leaf water status (Farooq *et al*., 2009a). In this study, foliar application of Put and Spd increased the relative water content which may result in better drought tolerant.

Under water stress, reactive oxygen species (ROS) accumulation leads to damage of lipid membrane lipid (Radhakrishnan and Lee, 2013). Thus, cell membrane injury is induced (Bajji, 2000a). In this study, the application of all PAs improved membrane stability as indicated by decreasing electrolyte leakage under drought stress. PAs are known as a positively charged, which bound to negatively charged molecules, therefore, help to stabilize the membrane under stress conditions (Zhao and Yang, 2008; Xu, *et al*., 2011). Under drought stress, leaf rolling is an important response for increasing stomatal resistance to decreased leaf water potential (O'Toole and Cruz, 1980). Leaf rolling may be used as indicator of leaf water potential in rice. Blum (1988) reported the use of leaf rolling under water stress as important selection criteria for dehydration avoidance. In this study, drought significantly increased leaf rolling compare to the droughted plants. Foliar spray with all PAs decreased leaf rolling. Asim *et al.* (2002) also reported that PAs are linked specifically to mechanisms of adaptation to water deficit stress by decreasing the degree of leaf rolling in plants during drought stress.

Drought causes effects on chlorophyll contents in plants. The present study showed that drought stress caused reduction in chlorophyll contents. However, exogenous application of Spm significantly improved chlorophyll *a*, *b* and total chlorophyll contents under drought stress. Foliar spray with PAs was also reported to increase drought tolerance of rice by improving photosynthesis (Farooq *et al*., 2009a). Accumulation of sucrose can enhance osmotic balance under drought stress (Farooq *et al*., 2009b). In this study, foliar spray with PAs also increasessucrose and fructose content in the droughted plants. Zhao *et al.* (2009) also reported that exogenous Put improved drought tolerance of wheat by increasing accumulation of soluble sugar in leaves. Sucrose is an energy source and plays an important role in stabilization of cell membrane under drought stress (Zhou and Yu, 2010). Osmotic adjustment is a mechanism of drought adaptation for maintain structural and improved function of cell components under drought stress in plants (Sanders and Arndt, 2012). Li *et al.* (2014) reported that Spd was correlated with organic solutes accumulation in response to water stress. In addition, accumulation of sugars was also coincided with increasing SPS activities under drought stress. It can be suggested that PAs induced increase of leaf relative water content, chlorophyll content, accumulation of sucrose, fructose content and SPS activities which alleviate the effects of drought stress.

In conclusion, this study demonstrates that accumulation of sugar and other carbohydrate were associated with drought stress. Exogenous application of PAs was also shown to improve better drought tolerant by enhancing accumulation of sugar and other carbohydrate under drought stress.

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