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.

Acknowledgements

This study was granted by department of Biology, faculty of Science and supported by the Salt-tolerance rice research group, Khon Kaen University, Thailand.

References

Arnon DI. Copper enzyme in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris.* Plant Physiology 1949; 24: 1-15.

Asim K, Rabiye T, Narcin PU, Neslihan S. Effect of polyamines on leaf rolling during drought stress in *Ctenanthe setosa* (Rosc.) Eichler. Journal of Plant Sciences 2002; 50: 1-19.

Bajji M, Lutts S, Kinet, JM. Physiological changes after exposure to and recovery from polyethylene glycol-induced water deficit in callus cultures issued from durum wheat (*Triticum durum* Desf.) cultivars differing in drought resistance. Journal of Plant Physiology 2000a; 156: 75–83.

Baninasab B, Ghobadi C. Influence of paclobutrazol and application methods on hightemperature stress injury in cucumber seedlings. Journal of Plant Growth regulation 2011; 30: 213-219.

Blum A. Plant breeding for stress environments. USA: Florida CRC press inc; 1988.

Bradford MM. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein dye-binding. Analytical Biochemistry 1976; 72: 248-254.

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F. Colorimetric method for determination of sugars and related substances. Analytical Chemistry 1956; 28: 350-356.

Evans PT, Malmberg RL. Do polyamines have roles in plant development. Annual Review of Plant Physiology and Plant Molecular Biology 1989; 40: 235–269.

Farooq M, Wahid A, Lee DJ. Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. Acta Physiologiae Plantarum 2009; 31: 937-945.

Farooq M, Wahid DJ, Lee O. Advance in drought resistance of rice. Critical Reviews in Plant Sciences 2009b; 28: 199-217.

Gupta K, Dey A, Gupta B. Plant polyamines in abiotic stress responses. Acta Physiologiae Plantarum 2013; 35: 2015-2036.

IRRI. Research Institute. Annual Report for 1975. Los Banos: Philippines, 1976.

Li Z, Peng Y, Zhang XQ, Pan MH. Ma X, Huang LK. and Yan YH. Exogenous spermidine improves water stress tolerance of white clover (*Trifolium repens* L.) involved in antioxidant defence, gene expression and proline metabolism. Plant Osmic Journal 2014; 6: 517-526.

Liu F, Jensen CR, Anderson MN. A review of drought adaptation in crop plants: changes in vegetative and reproductive physiology induced by ABA-based chemical signals. Australian Journal of Agricultural Research 2005; 56: 1245-1252.

Madore MA. Carbohydrate mrtabolism in photosynthetic and nonphotosynthetic tissues of variegated leaves of Coleus blumei. Plant Physiology 1990; 93: 617-622.

Moschou PN, Sanmartin M, Andriopoulou AH. Bridging the gap between plant and mammalian polyamine catabolism: a novel peroxisomal polyamine oxidase responsible for a full back-conversion pathway in Arabidopsis. Plant physiology 2008; 147(4): 1845-1857.

O'Toole CJ, Cruz TR. Response of Leaf Water Potential, Stomatal Resistance, and Leaf Rolling to water Stress. Plant Physiology 1980; 65: 428-432.

Pattanagul W. Exogenous Abscisic Acid Enhances Sugar Accumulation in Rice (*Oryza sativa* L.) under Drought stress. Asian Journal of Plant Sciences 2011; 1-8.

Pottosin I, Shabala S. Polyamines control of cation transport across plant mem-branes: implications for ion homeostasis and abiotic stress signalling. Frontiers in Plant Science 2014; 5: 154.

Radhakrishnan R, Lee IJ. Ameliorative effects of spermine against osmotic stress through antioxidants and abscisic acid changes in soybean pods and seeds. Acta Physiology plant 2013; 35: 263-269.

Robbins NS, Pharr DM. Regulation of photosynthetic carbon metabolism in cucumber by light intensity and photosynthetic period. Plant Physiology 1987; 85: 592-597.

Sanders GJ, Arndt SK. Osmotic Adjustment Under Drought Conditions. In: Aroca R, editiors. Plant Responses to Drought Stress. Australia; 2012. pp. 199-229.

Tun NN, Catarina SC, Bequm T, Silveira V, Handro W, Floh EI, Scherer GF. Polyamines induce rapid biosynthesis of nitric oxide (NO) in *Arabidopsis thaliana* seedlings. Plant Cell Physiology 2006; 47: 346–354.

Turner NC. Techniques and experimental approaches for the measurement of plant water status. Plant soil 1981; 58: 339-366.

Turner NC. Adaptation to water deficits – a changing perspective. Australian Journal of Plant Physiology 1986; 13: 175–190.

White DA, Turner NC, Galbraith JH. Leaf water relations and stomatal behaviour of four allopatric *Eucalyptus* species planted in Mediterranean southwestern Australia. Tree Physiology 2000; 20: 1157–1165.

Xu X, Shi G, Ding C, Xu Y, Zhao J, Yang H, Pan Q. Regulation of exogenous spermidine on the reactive oxygen species level and polyamine metabolism in *Alternanthera philoxeroides* (Mart.) Griseb under copper stress. Plant Growth Regulation 2011; 63:251–258.

Xu S, Li J, Zhang X, Wei H, Cui L. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat stress. Environmental and Experimental Botany 2006; 56: 274–285.

Zhao HZ, Yang HQ. Exogenous polyamines alleviate the lipid peroxidation induced by cadmium chloride stress in *Malus hupehensis* Rehd. Scientia Horticulturae 2008; 116: 442-447.

Zhao WC, Li H, Zhao HJ, Han YL, Tan JF. Effects of exogenous polyamine osmotica regulation in wheat seedling leaves under drought stress. Chinese Science Bulletin 2009; 25:148–151.

Zhou Q, Yu B. Changes in content of free, conjugated and bound polyamines and osmotic adjustment in adaptation of vetiver grass to water deficit. Plant Physiology and Biochemistry 2010; 48: 417–425.

Zlatev Z, Lidon FJC. An overview on drought induced changes in plant growth, water relations and photosynthesis. Emirates Journal of Food and Agriculture 2012; 24: 57-72.