
Genotypic Variation in Proline Accumulation during Sequential Drought and Rewatering in Response to Drought Preconditioning

Duangpan, S.^{1,2*}, Sujitto, S.¹ and Eksomtramage, T.^{1,2}

¹Department of Plant Science, Faculty of Natural Resources, Prince of Songkla University, Songkhla, 90112 Thailand; ²Oil Palm Agronomical Research Center, Faculty of Natural Resources, Prince of Songkla University, Songkhla, 90112 Thailand.

Duangpan, S., Sujitto, S. and Eksomtramage, T. (2017). Genotypic variation in proline accumulation during sequential drought and rewatering in response to drought preconditioning. *International Journal of Agricultural Technology* 13(6):927-940.

Abstract The correlation between stress-induced proline accumulation and stress tolerance has been reported in multiple crops. In oil palm, elevated proline content was observed but the detailed study on this regard is still limited. The objective was to elucidate the effects of genotypes and drought preconditioning on proline accumulation in oil palm seedling under drought stress and rewatering. Two tenera hybrid progenies, PSU-106 (drought tolerant progenies) and PSU-220 (drought sensitive progenies) showed that the increased proline level under drought stress was proved. In non-preconditioned seedlings, PSU-106 accumulated higher concentration of proline compared to PSU-220. However, drought preconditioning elevated the maximum proline accumulation in PSU-220 to comparable level to PSU-106. In rewatering period, proline content was promptly reduced to the level equivalent to the concentration before stress in all treatments, but the reduction rate was delayed in drought-preconditioned PSU-106 progenies. This demonstrated that proline accumulation in response to drought stress in oil palm was genotype-dependent and drought-preconditioning enhanced proline accumulation in sensitive genotype, but not in tolerant genotype.

Keywords: Oil palm, Proline, Preconditioning, Drought stress

Introduction

Oil palm is a tropical oil crop grown primarily as a supplier for industrial production of vegetable oil (Euler *et al.*, 2017). Commercial oil palm is originally from West Africa but the plantation nowadays is centred in Southeast Asia especially in Indonesia and Malaysia which together contribute more than 80% of global oil palm fruit production (Vijay *et al.*, 2016). Total oil palm plantation in Indonesia, the world chief producer, is currently 8 million ha and expected to increase to 13 million ha by the year 2020 (Ferrianta, 2017). Thailand ranked the third place with the plantation area of 560,000 ha in 2008

* **Coressponding author:** Duangpan, S.; **Email:** saowapa.d@psu.ac.th

and reached 636,800 ha in 2013 (Taeprayoon *et al.*, 2015). Overall, the oil palm industry is predicted to expand continuously due to the growing demand of edible oil (Vijay *et al.*, 2016).

In commercial oil palm plantation, drought exacerbated by climate change becomes a major limiting factor (Murray *et al.*, 2012; Paterson *et al.*, 2015). In general, optimal growth condition for oil palm requires annual rainfall of over 2,000 mm distributed evenly during the year (Corley and Tinker, 2003; Hartley, 1989). Minimum rainfall for oil palm growth is 1,250 mm with no marked dry period (Pirker *et al.*, 2016). Oil palm plantation with water scarcity significantly reduces growth and oil yield (Cao *et al.*, 2011; Carr, 2011; Legros *et al.*, 2009). In addition, low level of water availability affects oil palm inflorescence initiation and differentiation, resulting in a decreased proportion of female flowers and therefore fruit bunch productivity (Corley and Tinker, 2003; Forero *et al.*, 2012).

To cope with drought, plants have adopted several physiological responses. In addition to decline in key physiological processes such as stomatal conductance, leaf water potential and net photosynthesis, drought induces the increase level of osmoprotectants (i.e. proline, polyol and glycinebetaine) to adjust the intracellular osmotic potential and avoid cell injury (Bartels and Sunkar, 2005; Chaves *et al.*, 2003). Among many different kinds of osmolytes, proline is one of the major osmotic molecules reported to accumulate during drought period in multiple species, for example, potato, tomato, wheat, rice, citrus and coconut (Hien *et al.*, 2003; Schafleitner *et al.*, 2007; Sharma *et al.*, 2017; da Silva *et al.*, 2016; Zandalinas *et al.*, 2016). Proline is able to protect cells from damage by functioning as both an osmotic agent and a radical scavenger. Besides, the correlation between drought tolerance ability and proline content in response to osmotic stress has been documented (Hien *et al.*; 2003, Kishor and Sreenivasulu, 2014). Drought tolerant genotypes appeared to accumulate higher amount of proline compare to the sensitive genotypes (Hien *et al.*, 2003, Mwadzingeni *et al.*, 2016). In fact, proline accumulation has long been proposed to be useful as a complementary strategy for selection of drought tolerant genotypes in plant breeding. In oil palm, elevated proline content during stress has been reported and could be regarded as a criterion for screening for stress tolerance (Cha-um *et al.*, 2013; Jazayeri *et al.*, 2015). However, more detail is needed to understand the mechanism underlying proline accumulation in oil palm so that using proline level during stress period as indicator for stress tolerance and manipulation of proline accumulation for increasing stress tolerance strength can be appropriately applied. Therefore, the aim of this study was to investigate the

effects of genotypes and drought preconditioning on proline accumulation behaviour in response to drought stress and rewatering in oil palm seedling.

Materials and methods

Plant materials

Two *tenera* hybrid progenies, PSU-106 and PSU-220, developed at Prince of Songkla University, Songkhla, Thailand, by crossing two different selected *dura* (female parent) palms and one common *pisifera* (male parent) palm were used in this study. According to our previous study, PSU-106 was identified to be drought tolerant as the seedlings were able to maintain the highest growth and exhibit superior physiological performance in moderate and severe drought stresses when compared to other progenies. In contrast, PSU-220 was among the progenies with poorest growth and physiological traits and, therefore, identified as drought sensitive progeny (Sujitto, 2016). The study was carried out using 9-month old PSU-106 and PSU-220 seedlings in a greenhouse condition. Seedlings were selected according to their uniformity in size.

Preconditioning and stress treatments

The following preconditioning treatments were imposed to the selected seedlings of PSU-106 and PSU-220 progenies, T-0 (control treatment), irrigated daily at 100% of field capacity; T-1, irrigated every 4 days at 100% of field capacity; T-2, irrigated every 8 days at 100% of field capacity. Seedlings were maintained under these preconditioning conditions for 24 days followed by full irrigation for 5 days. As a consequent, T1 and T2 seedlings were subjected to 6 and 3 cycles of drought, respectively. Drought-preconditioned and non-preconditioned seedlings were subsequently exposed to drought stress for 10 days and rewatered for 5 days.

Soil moisture content

Soil moisture content was measured daily during the preconditioning, drought stress and rewatering periods. Three pots from each treatment were sampled and soil moisture content was measured at 10 cm depth using Delta-T WET-2 soil moisture meter.

Proline analysis

Proline content was measured as described by (Bates *et al.*, 1973). A total of 0.05 g ground, frozen leaf tissue was extracted in 10 ml of 3 % sulfosalicylic acid and filtered through filter paper (Whatman no. 1, England). After filtration, 1 ml of the supernatant was mixed with 1 ml of glacial acetic acid and ninhydrin reagent. The reaction mixture was incubated in a water bath at 100 °C for 1 h. and subsequently terminated by placing the tubes in an ice bath followed by mixing with 4 ml toluene. The absorbance at 520 nm was measured in a spectrophotometer. The proline concentration was determined from a standard curve and calculated on a fresh weight basis.

Experimental design and statistical analysis

The experiment was arranged in completely randomized design with 5 replications. One plant per replicate was used. The data were analysed using analysis of variance (ANOVA) at the significant level of 5%, followed by Least Significant Difference (LSD) test if there were significant differences among the treatments.

Results

Preconditioning period

During the preconditioning period, same patterns of soil moisture content fluctuation were observed in cultured pots of PSU-106 and PSU-220 progenies. Soil moisture contents in the control treatment (T-0) were in the range of 19.10 - 21.02%. In the T-1 and T-2 treatments, soil moisture content decreased continuously and restored to the initial level of soil moisture content following full irrigation on the basis of 4-day and 8-day intervals, respectively. Soil moisture content values of T-1 treatments fluctuated between 6.08% and 21.67%, whereas those of T-2 treatments gradually changed between 3.25% and 19.45%. Therefore, the lowest soil moisture contents of T-1 and T-2 treatments were 30.30% and 16.20% of field capacity, respectively (Figure 1).

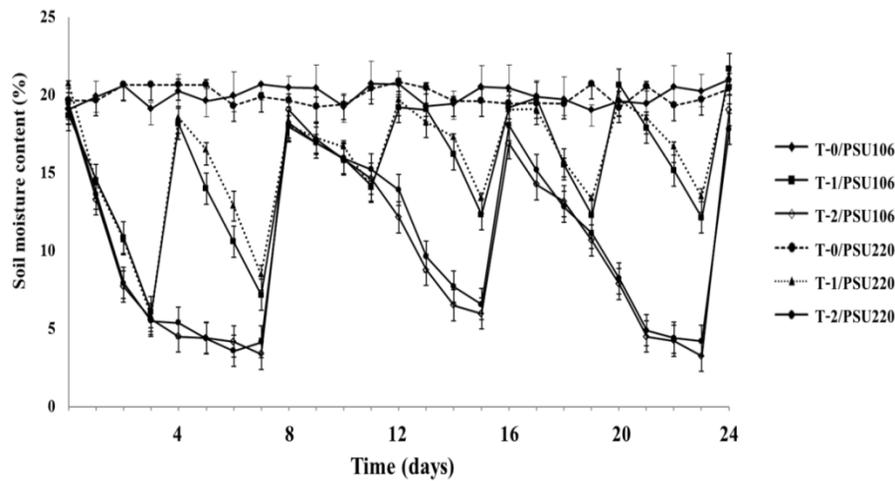


Figure 1. Soil moisture content in the control and two different drought-preconditioning conditions. T-0 (control treatment), irrigated daily at 100% of field capacity; T-1, irrigated every 4 days at 100% of field capacity; T-2, irrigated every 8 days at 100% of field capacity. Each point is the average of three replicates. Vertical bars on data points are \pm S.E.

Effects of different irrigation regimes and genotypes on leaf proline content were observed during preconditioning period. Oil palm seedlings in T-2 treatment accumulated the highest amount of proline followed by those in T-1 and control treatments, respectively (Figure 2). However, PSU-220 plants of T-1 treatments showed elevated but not significantly different proline content with those exposed to daily full irrigation. For PSU-106 progenies, the differences of proline contents among 3 irrigation regimes were statistically significant ($P < 0.05$). Considering the same irrigation treatments, proline levels did not differ across genotypes except for T-2 treatments. PSU-106 seedlings exposed to 8-day interval watering accumulated higher amount of proline than PSU-220 seedlings in the same drought preconditioning treatment. This indicates the genotypic variability of oil palm in adaptive response to different levels of water availability through proline accumulation.

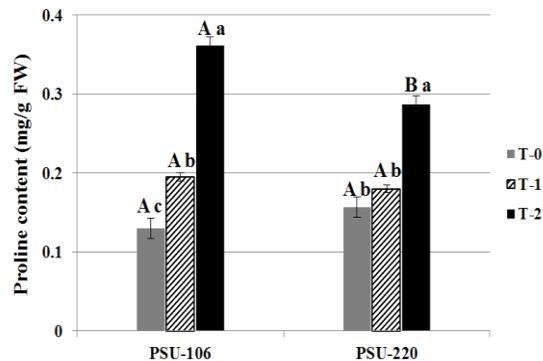


Figure 2. Proline content of PSU-106 and PSU-220 progenies under different preconditioning irrigation. Values are presented as means \pm S.E. (n = 5 replicates). Different small letters indicate significant difference ($P < 0.05$) of proline content between treatments within the same progeny. Different capital letters indicate significant difference ($P < 0.05$) of proline content between different progenies within the same preconditioning condition.

Drought stress and rewatering period

Prior to drought stress, oil palm seedlings were watered daily until soil moisture reached full saturation for 5 days. Oil palm seedlings were measured for proline content before being exposed to stress. Drought stress was performed by holding irrigation for 10 consecutive days. Soil moisture contents decreased gradually and reached $2.12 \pm 0.13\%$ across all treatments. Rewatering following drought stress brought the soil moisture content up to approximately 20% in all treatments.

Proline content was measured at 2 days interval during drought stress period and at 1, 3 and 5 days after resuming watering. Analysis of variance (ANOVA) of the effects of drought preconditioning treatment and genotypes on proline accumulation at different time points indicated that genotype significantly affected proline content during both drought and rewatering periods (Table 1). The effect of preconditioning treatment was significant for proline content during the first 8 days of drought but was diminished by day 10. During the recovering time, the significance of preconditioning treatment was inconsistent. In addition, proline levels were not consistently, significantly affected by genotype \times preconditioning treatment interaction.

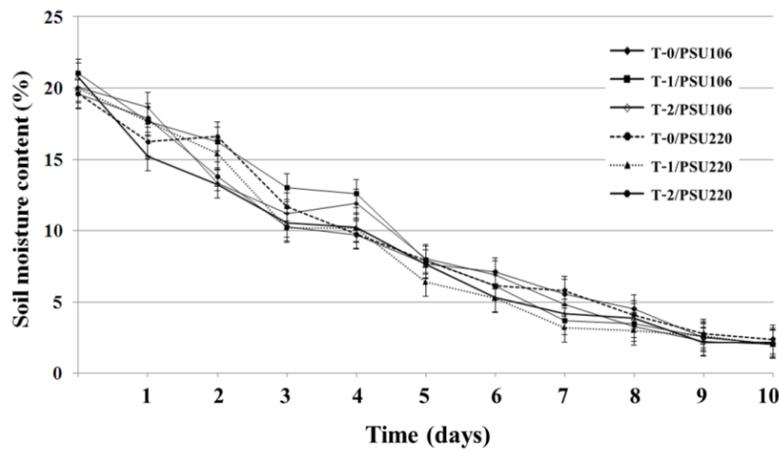


Figure 3. Soil moisture content during drought stress period. T-0 (control treatment), seedlings without preconditioned drought; T-1, seedlings exposed to preconditioned drought of 4-day interval irrigation; T-2, seedlings exposed to preconditioned drought of 8-day interval irrigation. Each point is the average of three replicates. Vertical bars on data points are \pm S.E.

Table 1. Analysis of variance of the effects of drought preconditioning treatment and genotypes on proline accumulation at different time points

	Genotypes (G)	Preconditioning treatment (PT)	G×PT
df	1	2	2
Drought stress			
Day 0	0.567ns	2.501ns	2.808ns
Day 2	36.748***	4.214*	3.703ns
Day 4	17.524***	22.458***	4.560*
Day 6	33.246***	5.664*	2.269ns
Day 8	5.236*	18.278***	4.146*
Day 10	6.397*	1.255ns	0.864ns
Rewatering			
Day 1	13.404***	2.911ns	3.670ns
Day 3	10.542***	18.913***	21.608***
Day 5	0.340ns	2.019ns	0.332ns

ns represents no significance, * represents significant difference at $P \leq 0.05$ and *** represents significant difference at $P \leq 0.001$.

The average proline content of PSU-106 and PSU-220 progenies during drought stress showed that drought induced the accumulation of proline in both progenies. The highest proline levels were observed 8 days after water withholding across all treatments and genotypes (Figure 3). During the drought stress, higher proline concentration was found in PSU-106 progenies. The differences were most pronounced in T-0 treatment (Figure 3A). Drought preconditioning improved proline accumulation of PSU-220 progenies in response to water deprivation. Therefore, the similar proline levels of PSU-106 and PSU-220 progenies were observed in T-1 and T-2 treatments along the drought period (Figure 3B and 3C). In PSU-106 progenies, severe drought preconditioning delayed the increasing level of proline when compare to control and moderate drought preconditioning treatment (Figure 4A). However, at 8 days after water withholding where the proline accumulation peaks were observed, the comparable amount of 0.82, 1.00 and 0.90 mg proline/g FW were measured in T-0, T-1 and T-2 treatments, respectively (Figure 4A). In PSU-220 progenies, drought preconditioning boosted the highest proline contents at day 8 of drought stress to 1.02 and 0.86 mg/g FW in T-1 and T-2 treatments, respectively, which were 1.9 and 1.5 folds compared to control treatment (Figure 4B).

In the rewatering period, genotypic differences were not detected in T-0 treatment. Early reduction of proline level was demonstrated in both PSU-106 and PSU-220 progenies without preconditioning (Figure 3A). Moderate and severe drought preconditioned PSU-106 progenies showed slower proline level decline compared to PSU-220 progenies (Figure 3B and 3C). In the first day of rewatering, proline concentration of PSU-106 progenies in T-0 treatment was reduced to 0.29 mg/g FW, while those in T-1 and T-2 treatments proline concentrations were recorded 0.45 and 0.56 mg/g FW, respectively (Figure 4A). Proline concentration in PSU-220 progenies of all three treatments responded faster and reduced to 0.26, 0.27 and 0.27 mg/g FW in T-0, T-1 and T-2 treatments, respectively (Figure 4B).

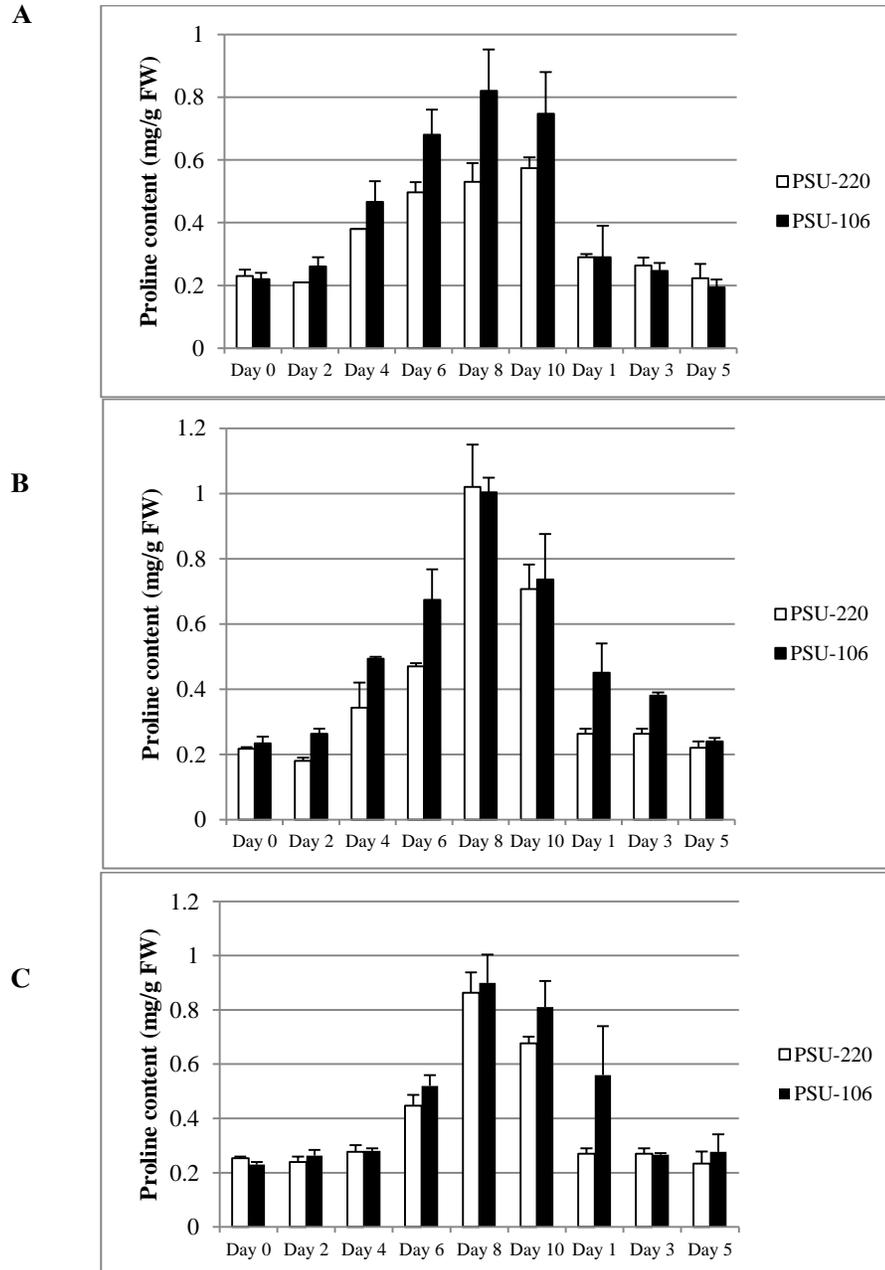


Figure 3. Proline content during drought stress and rewatering periods of PSU-106 and PSU-220 progenies previously exposed to three different preconditioning treatments including daily watering (A), 4-day interval irrigation (B) and 8-day interval irrigation (C). Drought stress was implemented for 10 days (Day 0 to Day 10) followed by rewatering for 5 days (Day 1 to Day 5). Values are presented as means \pm S.E. (n = 5 replicates).

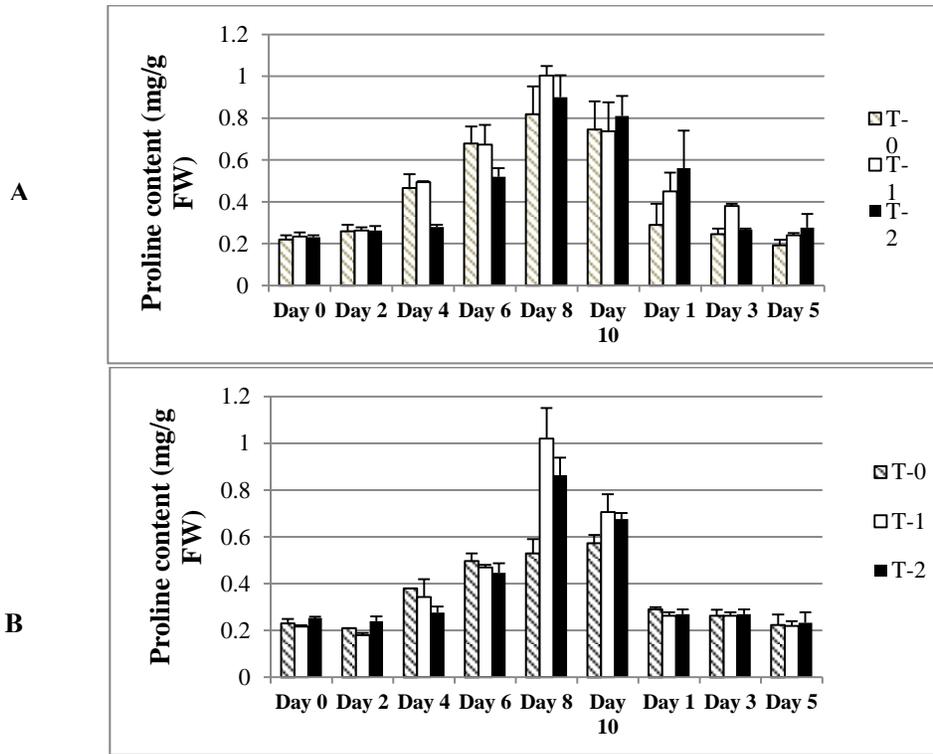


Figure 4. Proline contents of PSU-106 (A) and PSU-220 (B) progenies during drought stress and rewetting periods. Drought stress was implemented for 10 days (Day 0 to Day 10) followed by rewetting for 5 days (Day 1 to Day 5). Values are presented as means \pm S.E. (n = 5 replicates).

Discussion

Proline accumulation is the common response of plant to drought stress. The increase level of proline in cytoplasm has been reported to function as a typical osmoprotectant to maintain cell stability during cell dehydration by protecting cell membranes, proteins and metabolic machinery, therefore resulting in drought stress tolerance (Hayat *et al.*, 2012; Singh *et al.*, 2015; Verbruggen and Hermans, 2008). It is also well documented that the capacity of proline accumulation is dependent on genotype (Kusvuran and Dasgan, 2017; Zheng *et al.*, 2017). This present study, we chose two oil palm genotypes, PSU-106 and PSU-220 differing in drought tolerance as materials as, according to our previous study, PSU-106 was relatively drought-tolerant while PSU-220 was relatively drought-sensitive (Sujitto, 2016). It was observed in this study that proline contents was gradually increased in both oil palm genotypes in

response to drought and reached the maximum level after eight days of moisture deprivation where the soil moisture contents were reduced to approximately 15% of field capacity. This is in agreement with several studies in oil palm seedlings in which the increasing trend of proline content was demonstrated in oil palm leaves and roots in water deficit conditions (Azzeme *et al.*, 2016; Cao *et al.*, 2011; Cha-um *et al.*, 2013). Without drought preconditioning, the increased level of proline in relation to water deprivation is higher in the drought-tolerant PSU-106 than that in PSU-220. The greater proline accumulation could reflect the better osmotic adjustment capability resulting in stronger drought tolerance. In fact, correlation between the capacity of proline accumulation during water stress and drought tolerance in positive manner has been reported in several crops (Binott *et al.*, 2017; Ranganayakulu *et al.*, 2015). Man *et al.* (2011) studied drought tolerance in two tall fescue cultivars and demonstrated that the drought tolerant cultivar, Van Gogh, had greater levels of proline, ABA, and cytokinin content relative to the drought sensitive cultivar, AST7002, under water stress. Positive correlation between grain yield and proline content under drought stress conditions was evidenced in bread wheat genotypes (Mwadzingeni *et al.*, 2016). Additionally, Zu *et al.* (2017) reported that drought tolerance degree of 13 upland rices positively corresponded to high water potential, chlorophyll content and proline level. Therefore, according to the results of current study in oil palm, proline accumulation triggered by water restriction could be regarded as a criterion for drought tolerance in this species.

The effects of drought preconditioning on proline accumulation response of oil palm during water stress were also evaluated. Enhanced stress tolerance by prior exposure to mild or short period of stress has been elucidated in many crops (Hoffman *et al.*, 2012; Jiang and Huang, 2001). Preconditioning dramatically enhanced the maximum level of proline in relatively drought-sensitive PSU-220 exposed to prolonged period of drought stress. This could contribute to improved ability of plant to cope with drought stress by better protection of protein structure and free radical scavenging activity. The accumulation rate, however, was not affected as the highest proline content was observed 8 days after stress as that found in control treatment. During rewatering period, reduction of proline content was delayed in preconditioned PSU-106 indicating that the mechanism underlying recovering was modified. No alteration was observed in PSU-220 during this period. Preconditioning-elevated proline accumulation during subsequent stress has been reported in zucchini, poplar, rice and some other grass species (Bejaoui *et al.*, 2016; Carvajal *et al.*, 2015; Dias *et al.*, 2014; Hoffman, *et al.*, 2012; Jiang and Huang, 2001; Kumar *et al.*, 2008.). Those preconditioned plants maintained higher

growth, cell stability and less oxidative damage compared to non-preconditioned treatments therefore identified as higher tolerance. It should be noted that higher stress tolerance in preconditioned plant is associated with not only elevated proline content but also some other physiological and biochemical changes, for example, increased antioxidant enzyme activity and total ion (K^+ , Ca_2^+ , Na^+ , Mg_2^+ , Cl^- , and P) concentration (Carvajal *et al.*, 2015; Jiang and Huang, 2001). In oil palm, apart from proline accumulation, other preconditioning-induced physiological and biochemical changes are needed to investigate.

Acknowledgements

This work was supported by the Higher Education Research Promotion and National Research University Project of Thailand, Office of the Higher Education Commission and Oil Palm Agronomical Research Center: Phase 2, Faculty of Natural Resources, Prince of Songkla University.

References

- Azzeme, A. M., Abdullah, S. N. A., Aziz, M. A. and Wahab, P. E. M. (2016). Oil palm leaves and roots differ in physiological response, antioxidant enzyme activities and expression of stress-responsive gene upon exposure to drought stress. *Acta Physiologiae Plantarum* 38:1-12.
- Bartels, D. and Sunkar, R. (2005). Drought and salt tolerance in plants. *Critical Reviews in Plant Sciences* 24:23-58.
- Bates, L. S., Waldren, R. P. and Teare, I. D. (1973). Rapid determination of free proline for water-stress studies. *Plant and Soil* 39:205-207.
- Bejaoui, Z., Mguis, K., Abassi, M., Albouchi, A. and Lamhamedi, M. S. (2016). Involvement of carbohydrates in response to preconditioning flooding in two clones of *Populus deltoides* Marsh. x *P. nigra* L. *Journal of Plant Growth Regulation* 35:492-503.
- Binott, J. J., Owuochi, J. O. and Bartels, D. (2017). Physiological and molecular characterization of Kenyan barley (*Hordeum vulgare* L.) seedlings for salinity and drought tolerance. *Euphytica* 213:139.
- Cao, H. X., Sun, C. X., Shao, H. B. and Lei, X. T. (2011). Effects of low temperature and drought on the physiological and growth changes in oil palm seedlings. *African Journal of Biotechnology* 10:2630-2637.
- Carr, M. K. V. (2011). The water relations and irrigation requirements of oil palm (*Elaeis guineensis*): A review. *Experimental Agriculture* 47:629-652.
- Carvajal, F., Palma, F., JAMILENA, M. and Garrido, D. (2015). Preconditioning treatment induces chilling tolerance in zucchini fruit improving different physiological mechanisms against cold injury. *Annals of Applied Biology* 166:340-354.
- Cha-um, S., Yamada, N., Takabe, T. and Kirdmanee, C. (2013). Physiological features and growth characters of oil palm (*Elaeis guineensis* Jacq.) in response to reduced water-deficit and rewatering. *Australian Journal of Crop Science* 7:432-439.

- Chaves, M. M., Maroco, J. P. and Pereira, J. S. (2003). Understanding plant responses to drought - from genes to the whole plant. *Functional Plant Biology* 30:239-264.
- Corley, R. H. V. and Tinker, P. B. (2003). *The oil palm* 4th edition. Oxford: Blackwell Publishing.
- da Silva, A. R. A., Bezerra, F. M. L., de Lacerda, C. F., Miranda, R. D., Marques, E. C. and Gomes, E. (2016). Organic solutes in coconut palm seedlings under water and salt stresses. *Revista Brasileira de Engenharia Agrícola e Ambiental* 20:1002-1007.
- Dias, M. C., Oliveira, H., Costa, A. and Santos, C. (2014). Improving elms performance under drought stress: The pretreatment with abscisic acid. *Environmental and Experimental Botany* 100:64-73.
- Euler, M., Krishna, V., Schwarze, S., Siregar, H. and Qaim, M. (2017). Oil palm adoption, household welfare, and nutrition among smallholder farmers in Indonesia. *World Development* 93:219-235.
- Ferrianta, Y. (2017). Issue and solutions palm oil industry in Indonesia. *Agricultural Research and Technology* 5:1-2.
- Forero, D. C., Hormaza, P. and Romero, H. M. (2012). Phenological growth stages of African oil palm (*Elaeis guineensis*). *Annals of Applied Biology* 160:56-65.
- Hartley, C. W. S. (1989). *The oil palm* 3rd edition. Essex, England: Longman Scientific and Technical.
- Hayat, S., Hayat, Q., Alyemini, M. N., Wani, A. S., Pichtel, J. and Ahmad, A. (2012). Role of proline under changing environments: A review. *Plant Signaling and Behavior* 7:1456–1466.
- Hien, D. T., Jacobs, M., Angenon, G., Hermans, C., Thu, T. T., Van Son, L. and Roosens, N. H. (2003). Proline accumulation and Delta(1)-pyrroline-5-carboxylate synthetase gene properties in three rice cultivars differing in salinity and drought tolerance. *Plant Science* 165:1059-1068.
- Hoffman, L., Da Costa, M., Ebdon, J. S. and Zhao, J. Z. (2012). Effects of drought preconditioning on freezing tolerance of perennial ryegrass. *Environmental and Experimental Botany* 79:11-20.
- Jazayeri, M. D., Rivera, Y. D., Camperos-Reyes, J. E. and Romero, H. M. (2015). Physiological effects of water deficit on two oil palm (*Elaeis guineensis* Jacq.) genotypes. *Agronomía Colombiana* 33:164-173.
- Jiang, Y. W. and Huang, B. R. (2001). Osmotic adjustment and root growth associated with drought preconditioning-enhanced heat tolerance in Kentucky bluegrass. *Crop Science* 41:1168-1173.
- Kishor, P. B. K. and Sreenivasulu, N. (2014). Is proline accumulation *per se* correlated with stress tolerance or is proline homeostasis a more critical issue?. *Plant Cell and Environment* 37:300-311.
- Kumar, V., Shriram, V., Nikam, T. D., Jawali, N. and Shitole, M. G. (2008). Sodium chloride-induced changes in mineral nutrients and proline accumulation in Indica rice cultivars differing in salt tolerance. *Journal of Plant Nutrition* 31:1999-2017.
- Kusvuran, S. and Dasgan, H. Y. (2017). Effects of drought stress on physiological and biochemical changes in *Phaseolus vulgaris* L. *Legume Research* 40:55-62.
- Legros, S., Mialet-Serra, I., Caliman, J. P., Siregar, F. A., Clement-Vidal, A. and Dingkuhn, M. (2009). Phenology and growth adjustments of oil palm (*Elaeis guineensis*) to photoperiod and climate variability. *Annals of Botany* 104:1171-1182.
- Man, D., Bao, Y. X., Han, L. B. and Zhang, X. Z. (2011). Drought tolerance associated with proline and hormone metabolism in two tall fescue cultivars. *Hortscience* 46:1027-1032.

- Murray, S. J., Foster, P. N. and Prentice, I. C. (2012). Future global water resources with respect to climate change and water withdrawals as estimated by a dynamic global vegetation model. *Journal of Hydrology* 448:14-29.
- Mwadingeni, L., Shimelis, H., Tesfay, S. and Tsilo, T. J. (2016). Screening of bread wheat genotypes for drought tolerance using phenotypic and proline analyses. *Frontiers in Plant Science* 7:1276.
- Paterson, R. R. M., Kumar, L., Taylor, S. and Lima, N. (2015). Future climate effects on suitability for growth of oil palms in Malaysia and Indonesia. *Scientific Reports* 5:14457.
- Pirker, J., Mosnier, A., Kraxner, F., Havlik, P. and Obersteiner, M. (2016). What are the limits to oil palm expansion? *Global Environmental Change-Human and Policy Dimensions* 40:73-81.
- Ranganayakulu, G. S., Sudhakar, C. and Reddy, P. S. (2015). Effect of water stress on proline metabolism and leaf relative water content in two high yielding genotypes of groundnut (*Arachis hypogaea* L.) with contrasting drought tolerance. *Journal of Experimental Biology and Agricultural Sciences* 3:97-103.
- Sujitto, S. (2016). Screening for drought tolerance in oil palm seedling genotypes (Master's Thesis) Prince of Songkla University.
- Schafleitner, R., Gaudin, A., Rosales, R. O. G., Aliaga, C. A. A. and Bonierbale, M. (2007). Proline accumulation and real time PCR expression analysis of genes encoding enzymes of proline metabolism in relation to drought tolerance in Andean potato. *Acta Physiologiae Plantarum* 29:19-26.
- Sharma, M., Gupta, S. K., Majumder, B., Maurya, V. K., Deeba, F., Alam, A. and Pandey, V. (2017). Salicylic acid mediated growth, physiological and proteomic responses in two wheat varieties under drought stress. *Journal of Proteomics* 163:28-51.
- Singh, M., Kumar, J., Singh, S., Singh, V. P. and Prasad, S. M. (2015). Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. *Reviews in Environmental Science and Bio-Technology* 14:407-426.
- Taepayoon, P., Tanya, P., Lee, S. and Srinives, P. (2015). Genetic background of three commercial oil palm breeding populations in Thailand revealed by SSR markers. *Australian Journal of Crop Science* 9:281-288.
- Verbruggen, N. and Hermans, C. (2008). Proline accumulation in plants: a review. *Amino Acids* 35:753-759.
- Vijay, V., Pimm, S. L., Jenkins, C. N. and Smith, S. J. (2016). The impacts of oil palm on recent deforestation and biodiversity Loss. *Plos One* 11:19.
- Zandalinas, S. I., Rivero, R. M., Martinez, V., Gomez-Cadenas, A. and Arbona, V. (2016). Tolerance of citrus plants to the combination of high temperatures and drought is associated to the increase in transpiration modulated by a reduction in abscisic acid levels. *BMC Plant Biology* 16:105.
- Zheng, H. F., Zhang, X., Ma, W. J., Song, J. Y., Rahman, S. U., Wang, J. H. and Zhang, Y. (2017). Morphological and physiological responses to cyclic drought in two contrasting genotypes of *Catalpa bungei*. *Environmental and Experimental Botany* 138:77-87.
- Zu, X., Lu, Y., Wang, Q., Chu, P., Miao, W., Wang, H. and La, H. (2017). A new method for evaluating the drought tolerance of upland rice cultivars. *The Crop Journal* 5:488-498.

(Received: 13 September 2017, accepted: 30 October 2017)