African Journal of Biotechnology Vol. 9(39), pp. 6509-6516, 27 September, 2010
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB10.809
ISSN 1684–5315 © 2010 Academic Journals

*Full Length Research Paper*

# Osmotic potential, photosynthetic abilities and growth characters of oil palm (*Elaeis guineensis* Jacq.) seedlings in responses to polyethylene glycol-induced water deficit

**Suriyan Cha-um[1]*, Teruhiro Takabe[2,3], Chalermpol Kirdmanee[1]**

[1]National Center for Genetic Engineering and Biotechnology (BIOTEC), National Science and Technology Development Agency (NSTDA), 113 Thailand Science Park, Paholyothin Road, Klong 1, Klong Luang, Pathumthani 12120, Thailand.
[2]Graduate School of Environmental and Human Sciences, Meijo University, Nagoya 468-8502, Japan.
[3]Research Institute, Meijo University, 1-501 Shiogamaguchi, Tenpaku-ku, Nagoya 468-8502, Japan.

Accepted 26 August, 2010

**The aim of the present study is to investigate the biochemical, physiological and morphological responses of oil palm seedlings when exposed to polyethylene glycol (PEG)-induced water deficit. Oil palm seedlings were photo-autotrophically grown in MS media and subsequently exposed to -0.23 (control), -0.42, -0.98 or -2.15 MPa PEG-induced water deficit. Osmotic potential ($\Psi_s$) in root and leaf tissues of oil palm seedlings grown under PEG-induced water deficit was decreased leading to chlorophyll degradation. Chlorophyll a ($Chl_a$), chlorophyll b ($Chl_b$), total chlorophyll (TC), total carotenoids ($C_{x+c}$), maximum quantum yield of photosystem II (PSII) ($F_v/F_m$) and photon yield of PSII ($\Phi_{PSII}$) in the oil palm seedlings under water deficit conditions dropped significantly in comparison to the control group, leading to a reduction in net-photosynthetic rate ($P_n$) and growth. A positive correlation between physiological and growth parameters, including osmotic potential, photosynthetic pigments and water oxidation in photosystem II and $P_n$ was demonstrated. These data provide the basis for the establishment of multivariate criteria for water deficit tolerance screening in oil palm breeding programs.**

**Key words:** Chlorophyll fluorescence, net-photosynthetic rate, pigment, water oxidation, water deficit stress.

## INTRODUCTION

Oil palm is one of the most oil production crops in the world and is widely cultivated in the tropical zone including Malaysia, Indonesia, Nigeria, Ivory Coast, Columbia and Thailand (Yusof and Chen, 2003; Wahid et al., 2005). Yield character, including oil yield and productivity, is the target of oil palm genetic improvement through a breeding program and biotechnology (Jalani et al., 1997; Cochard et al., 2005). Palm yield is dependent not only on genetic background, but also on environmental factors which include relative humidity,water availability, soil structure, fertilizer application, agricultural management and light conditions (Henson and Dolmat, 2003; Kallarackal et al., 2004; Henson and Harun, 2005). Abiotic stress tolerance including drought, salt-affected soil, extreme temperature, mineral deficiency and heavy metal toxicity is the alternative trait for oil palm improvement in the next step. Water available in the soil of oil palm plantations plays an important role for growth (Henson and Harun, 2005) and functions as a signal for female sex representation (Jones, 1997). In water shortage areas, there are a large number of male flowers as well as slow growth, prior to poor productivity. The basic information relating to water stress responses in oil

*Corresponding author. E-mail: suriyanc@biotec.or.th. Tel: (662) 564-6700. Fax: (662) 564-6707

palms is a hot issue which should be investigated further for water-deficit tolerance screening.

Water deficit is a major abiotic stress, which is widely distributed worldwide over 1.2 billion ha, especially in rain-fed areas (Chaves and Oliveira, 2004; Kijne, 2006; Passioura, 2007). The water deficit environment is reported as a key factor that limit plant growth and development prior to the loss of productivity, especially of crop species (Reddy et al., 2004; Blum, 2005; Neumann, 2008). Plant defense responses to water deficit such as transcription factors, water channels/transporters, hormonal regulation, osmoregulation and detoxification systems have been well published (Valliyodan and Nguyen, 2006; Seki et al., 2007; Cattivelli et al., 2008). Polyethylene glycol (PEG)-induced water deficit is well established and applied to screen drought tolerance in many plant species e.g pine (López et al., 2009), sunflower (Ahmad et al., 2009), wheat (Bayoumi et al., 2008) and potato (Gopal and Iwama, 2007). Physiological changes including reduced leaf water potential, pigment degradation, diminished chlorophyll a fluorescence, reduced net photosynthetic rate ($P_n$) and growth retardation prior to plant death when plants are exposed to water deficit stress have been widely investigated (Yordanov et al., 2003; Chaves and Oliveira, 2004; Reddy et al., 2004; Cattivelli et al., 2008). However, the basic knowledge concerning biochemical, physiological and morphological changes in the oil palm when exposed to water deficit is still limited. The aim of this study is to investigate the responses of the plant, in terms of osmotic potential, photosynthetic abilities and growth characters, to PEG-induced water deficit.

## MATERIALS AND METHODS

### Plant materials

Oil palm fruits were obtained from Suksomboon Palm Co Ltd. The kernel of the fruit was removed. The seeds with the seed coat were dried in a hot air oven at 45°C for 12 h, and then the seed coat was broken. The embryos, along with the endosperm were surface-disinfected once in 15% Clorox® for 20 min and once in 5% Clorox® for 30 min. The embryos were then excised to germinate in MS media (Murashige and Skoog, 1962). The media were adjusted to pH 5.7 before autoclaving. Oil palm seedlings were cultured *in vitro* under conditions of 25 ± 2°C ambient temperature, 60 ± 5% relative humidity (RH) and 60 ± 5 µmol $m^{-2}$ $s^{-1}$ photosynthetic photon flux density (PPFD) provided by fluorescent lamps with 16 $hd^{-1}$ photoperiod. After 2 months, the seedlings were transferred aseptically to MS-liquid sugar-free media. The uncovered vessels containing photoautotrophic seedlings were transferred aseptically to culture box chambers (Carry Box Model P-850, size 26 × 36 × 19 cm, Japan) with RH controlled at 65 ± 5% by 1.5 L saturated NaCl solution. The number of air exchanges in the culture box chambers was increased to 5.1 ± 0.3 $h^{-1}$ by punching the side of the plastic chambers with 32 holes and placing gas-permeable microporous polypropylene film (0.22 µm pore size) over the holes (Cha-um et al., 2003). Oil palm seedlings were acclimated for 14 days by placing the chambers in a plant growth incubator under a temperature shift of 28 ± 2°C/25 ± 2°C (light/dark), 500 ± 100 µmol $mol^{-1}$ $CO_2$ concentration, 60 ± 5% RH, 120 ± 5 µmol $m^{-2}$ $s^{-1}$ PPFD provided by fluorescent lamps with 16 $hd^{-1}$ photoperiod. Polyethylene glycol (PEG 6000) in the culture media was adjusted to -0.24 (0% PEG), -0.42 (1% PEG), -0.98 (2% PEG) or -2.15 MPa (3% PEG) water deficit for periods of 14 days. Root and leaf water potentials, photosynthetic pigments, chlorophyll fluorescence, net-photosynthetic rate ($P_n$) and growth characters were measured.

### Data measurements

Root and leaf osmotic potentials ($\Psi_s$) of oil palm seedlings were measured according to Lanfermeijer et al. (1991). 100 mg of fresh root and leaf tissues was cut into small pieces and transferred to 1.5 mL microtube, and then crushed by stirring with a glass rod. 20 µL of extracted solution were dropped directly onto a disc-shaped filter paper in an osmometer chamber (Wescor, Utah, USA).

Chlorophyll a ($Chl_a$), chlorophyll b ($Chl_b$) and total chlorophyll (TC), were analyzed following the methods of Shabala et al. (1998) and total carotenoid ($C_{x+c}$) concentrations were assayed according to Lichtenthaler (1987). 100 mg of leaf materials were collected and placed in a 25 mL glass vial, along with 10 mL 95.5% acetone, and blended using a homogenizer. The glass vials were sealed with parafilm to prevent evaporation, and then stored at 4°C for 48 h. $Chl_a$ and $Chl_b$ concentrations were measured using a UV-visible spectrophotometer at 662 and 644 nm wavelengths. The $C_{x+c}$ concentration was also measured by spectrophotometer at 470 nm. A solution of 95.5% acetone was used as blank. Chlorophyll fluorescence emission from the adaxial surface on the leaf was measured using a fluorescence monitoring system in the pulse amplitude modulation mode, as previously described by Loggini et al. (1999). A leaf adapted to dark conditions for 30 min using leaf-clips was initially exposed to the modulated measuring beam of far-red light (LED source with typical peak at wavelength 735 nm). Original ($F_0$) and maximum ($F_m$) fluorescence yields were measured under weak modulated red light (< 0.5 µmol $m^{-2}$ $s^{-1}$) with 1.6 s pulses of saturating light (> 6.8 µmol $m^{-2}$ $s^{-1}$ PAR) and calculated using FMS software for Windows®. The variable fluorescence yield ($F_v$) was calculated by the equation of $F_m$–$F_0$. The ratio of variable to maximum fluorescence ($F_v/F_m$) was calculated as maximum quantum yield of photosystem II (PSII) photochemistry. The photon yield of PSII ($\Phi_{PSII}$) in the light was calculated by $\Phi_{PSII} = (F_m'-F)/F_m'$ after 45 s of illumination, when steady state was achieved. In addition, non-photochemical quenching (NPQ) was calculated as described by Maxwell and Johnson (2000).

$P_n$ was calculated by comparing the different concentrations of $CO_2$ inside ($C_{in}$) and outside ($C_{out}$) the glass vessel containing the oil palm seedlings. The $CO_2$ concentrations at steady state were measured by gas chromatography (GC; Model GC-17A, Shimadzu Co. Ltd., Japan). The $P_n$ of *in vitro* cultivated seedlings was calculated according to the method of Fujiwara et al. (1987).

Shoot height (SH), root length (RL), leaf area (LA), fresh weight (FW) and dry weight (DW) of oil palm seedlings were measured. Oil palm seedlings were dried at 80°C in a hot-air oven for 2 days, and then incubated in desiccators before the measurement of dry weight. The leaf area of oil palm seedlings was measured using a Leaf Area Meter DT-scan.

### Experiment design

The experiment was arranged as Completely Randomized Design (CRD) with six replicates (n = 6). The mean values obtained were compared by Least Significant Difference (LSD) and analyzed using the Statistical Package for the Social Sciences (SPSS) software.

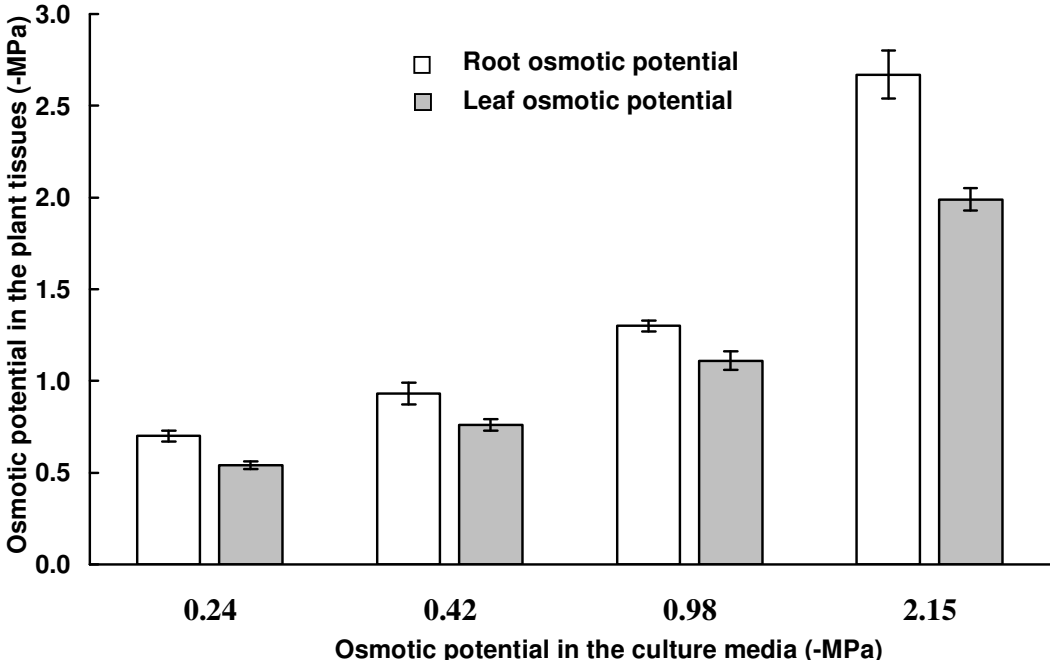


**Figure 1.** Root and leaf osmotic potentials of oil palm seedlings grown under PEG-induce water deficit for 14 days. Error bars are represented by ±SE.

The correlations between biochemical and physiological parameters were evaluated using Pearson's correlation coefficients.

## RESULTS AND DISCUSSION

Root and leaf osmotic potentials ($\Psi_s$) of oil palm seedlings were decreased in relation to the reduction in osmotic potential caused by PEG in the culture media (Figure 1). Compared to the control conditions ($\Psi_s$ = -0.238 MPa), $\Psi_s$ in the root and leaf tissues under extreme water deficit ($\Psi_s$= -2.15 MPa) declined by 3.7 and 3.8 times, respectively (Figure 1). A decreasing osmotic potential in the culture media containing PEG directly reduced the $\Psi_s$ in the root tissues (Figure 2A). Moreover, the decrease in root $\Psi_s$ was positively related to total chlorophyll degradation (Figure 2B). $Chl_a$, $Chl_b$, TC and $C_{x+c}$ levels in the leaf tissues dropped significantly when plants were exposed to water deficit stress, especially in $\Psi_s$ -2.15 MPa (Table 1). Under extreme water deficit conditions ($\Psi_s$ = -2.15 MPa), the $Chl_a$, $Chl_b$, TC and $C_{x+c}$ contents in the leaf tissues of oil palm seedlings were degraded for 24.3, 74.1, 49.6 and 25.7%, respectively. The $Chl_a$ and TC contents in the water deficit stressed leaves had correlation with maximum quantum yield of PSII ($F_v/F_m$) (Figure 3A) and photon yield of PSII ($\Phi_{PSII}$) (Figure 3B), respectively. The $F_v/F_m$, $\Phi_{PSII}$ and quantum efficiency of PSII (qP) in the leaf tissues of plants undergoing water deficit treatments decreased significantly, whereas non photochemical quenching (NPQ) increased, especially in extreme conditions ($\Psi_s$ = -2.15 MPa) leading to net photosynthetic rate ($P_n$) reduction (Table 2). A positive correlation between qP and $P_n$ was demonstrated in Figure 4A. Biochemical and physiological parameters including leaf $\Psi_s$, $Chl_a$, $Chl_b$, $C_{x+c}$, $F_v/F_m$, $\Phi_{PSII}$ and $P_n$ were found to have a positive correlation using Pearson's correlation coefficients (Table 3). In addition, $P_n$ was positively related to plant dry weight (Figure 4B). SH, RL, LA, FW and DW of water-deficit stressed seedlings were drastically inhibited in comparison to the control conditions (Table 4). Under extreme water deficit ($\Psi_s$ = -2.15 MPa), SH, RL, LA, FW and DW were reduced by 28.1, 63.8, 61.0, 65.6 and 46.7% when compared to the control.

Reduction on $\Psi_s$ in the root and leaf tissues of water-deficit oil palm seedlings was related to progressive water available in culture media containing PEG. It is quite similar to the report of Dwarf coconut palm in drought stress condition (Gomes et al., 2008). Photosynthetic pigments, $Chl_a$, $Chl_b$, TC and $C_{x+c}$, in the leaf tissues of oil palm seedlings were degraded, leading to diminution of $F_v/F_m$, $\Phi_{PSII}$, qP and $P_n$ in response to PEG-induced water deficit, especially in severe condition ($\Psi_s$ = -2.15 MPa). Although the decrease of TC content in response to water deficit is well known, different effects on $C_{x+c}$ have been reported for coconut (Gomes et al., 2008). In the case of oil palm, $C_{x+c}$ in the severe water deficit conditions was significantly degraded (25.7% of control) which

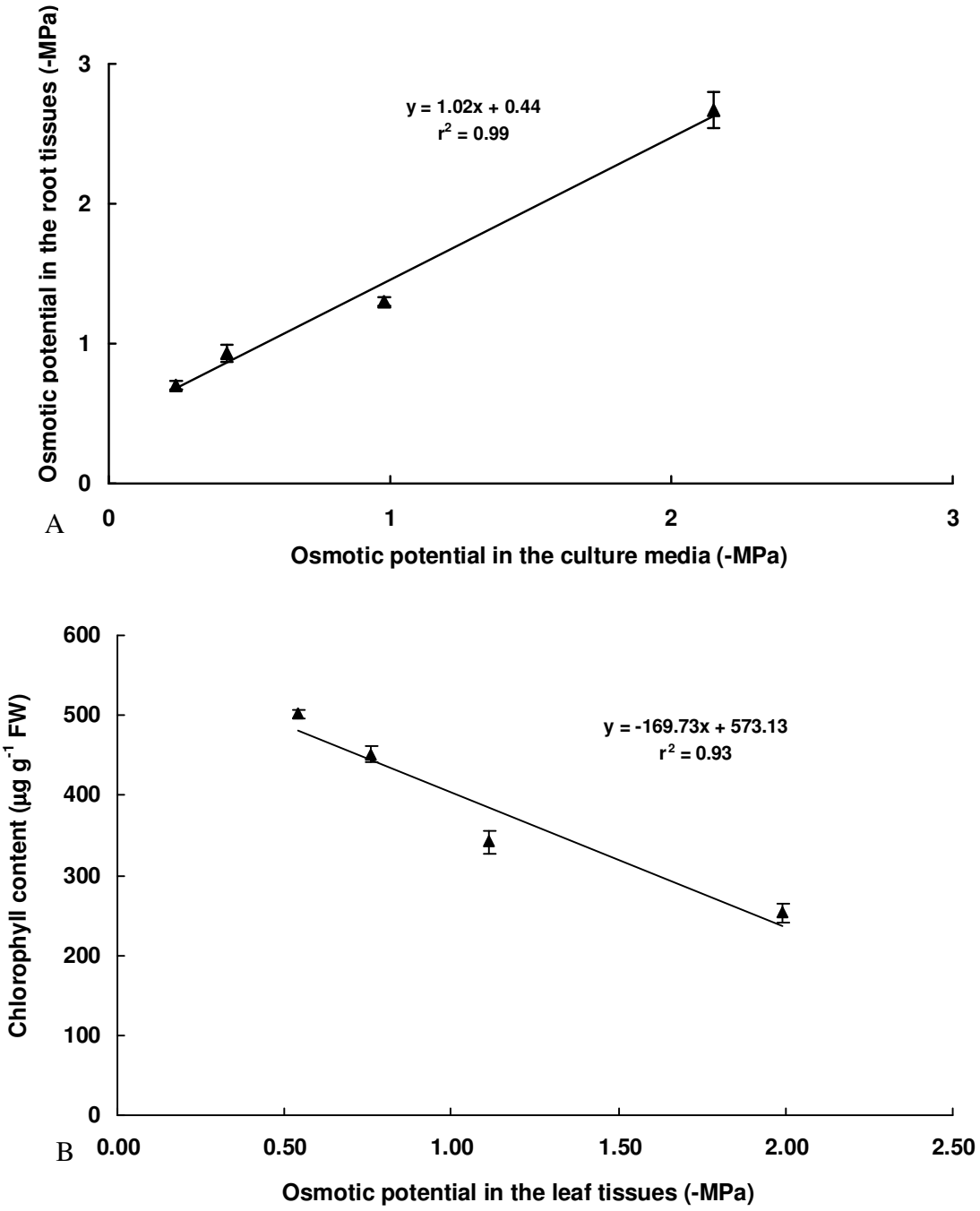


**Figure 2.** Relationship between osmotic potential in the culture media and osmotic potential in root tissues (A) and osmotic potential in the leaf tissues and total chlorophyll content (B) of oil palm seedlings grown under PEG-induced water deficit for 14 days. Error bars are represented by ±SE.

might cause the NPQ enrichment. The degree of the degradation of photosynthetic pigments and the $CO_2$ assimilation rate in response to severe water deficit are closely related to the diminution of $F_v/F_m$, $\Phi_{PSII}$ and $P_n$ reduction. Similar results have been reported in coconut (Gomes and Prado, 2007; Nainanayake, 2007; Gomes et al., 2008). In addition, $P_n$ in coconut palm is reduced significantly in both the Una (37.3% of water-well) and Jiqui cultivars (43.1% of water-well) when exposed to drought stress (Gomes et al., 2008) in order to limit the $CO_2$ assimilation rate through the stomatal apertures (Cornic, 2000). Growth performances in higher plants are

**Table 1.** Chlorophyll a ($Chl_a$), chlorophyll b ($Chl_b$), total chlorophyll (TC) and total carotenoids ($C_{x+c}$) contents of oil palm seedlings grown under PEG-induced water deficit for 14 days.

| Osmotic potential (-MPa) | $Chl_a$ (µ g $g^{-1}$FW) | $Chl_b$ (µ g $g^{-1}$FW) | TC (µ g $g^{-1}$FW) | $C_{x+c}$ (µ g $g^{-1}$FW) |
|---|---|---|---|---|
| 0.24 (Control) | 247.2a | 254.6a | 501.8a | 84.8a |
| 0.42 | 246.1a | 204.8b | 450.9b | 78.0ab |
| 0.98 | 228.9a | 112.6c | 341.5c | 73.5b |
| 2.15 | 187.1b | 65.9d | 253.0d | 63.0c |
| Significant level | ** | ** | ** | ** |

Different letters in each column show significant difference at $p \leq 0.01$ (**) by Least Significant Difference (LSD).

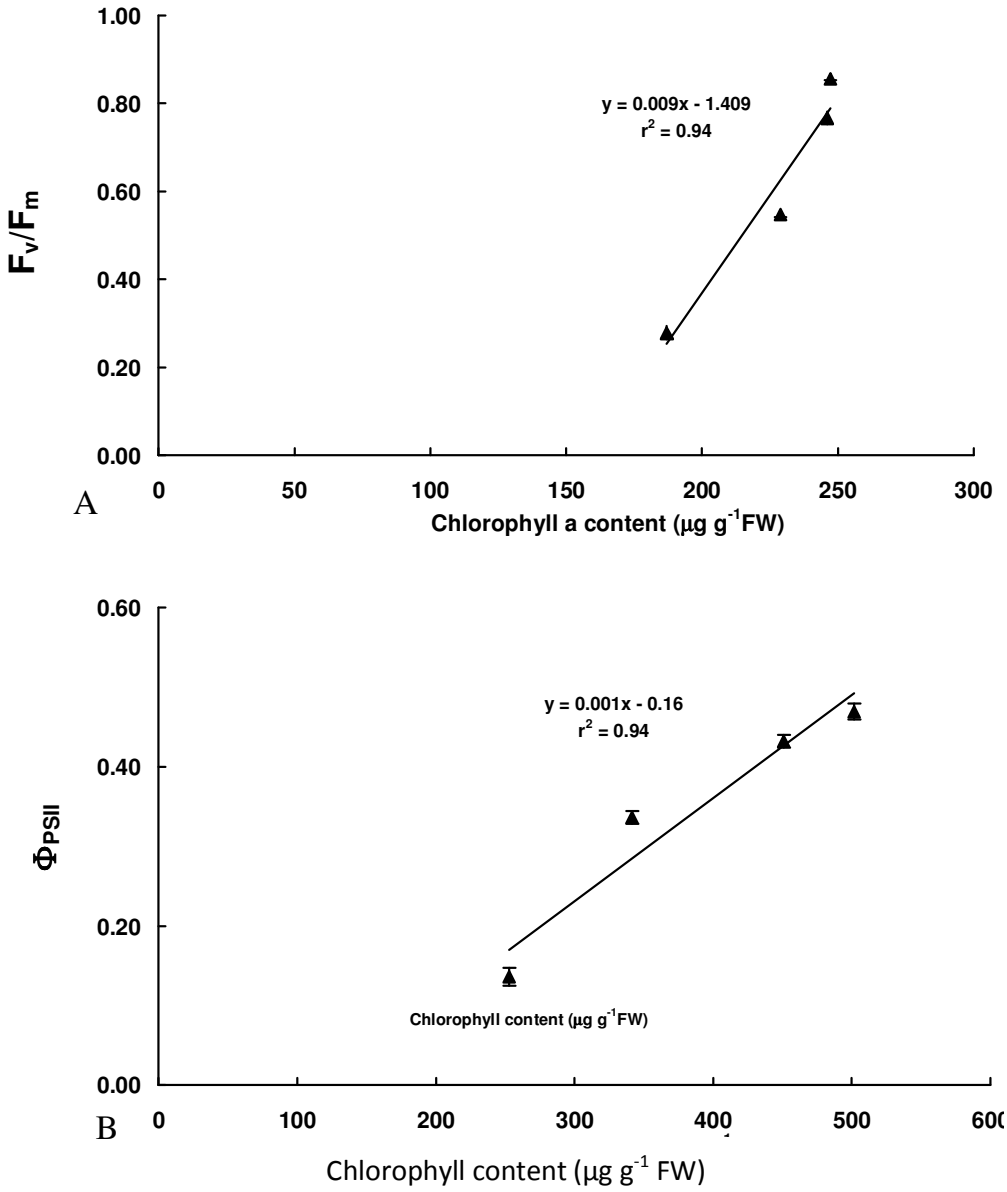


**Figure 3.** Relationship between chlorophyll a content and maximum quantum yield of PSII ($F_v/F_m$) (A) and total chlorophyll content and photon yield of PSII ($\Phi_{PSII}$) (B) of oil palm seedlings grown under PEG-induced water deficit for 14 days. Error bars are represented by ±SE.

**Table 2** Maximum quantum yield of PSII ($F_v/F_m$), photon yield of PSII ($\Phi_{PSII}$), quantum efficiency of PSII (qP), non-photochemical quenching (NPQ) and net photosynthetic rate ($P_n$) of oil palm seedlings grown under PEG-induced water deficit for 14 days.

| Osmotic potential (-MPa) | $F_v/F_m$ | $\Phi_{PSII}$ | qP | NPQ | $P_n$ (μ mol $m^{-2}$ $s^{-1}$) |
|---|---|---|---|---|---|
| 0.24 (Control) | 0.856a | 0.469a | 0.558a | 0.046d | 6.34a |
| 0.42 | 0.767b | 0.432a | 0.464b | 0.080c | 5.60a |
| 0.98 | 0.547c | 0.336b | 0.361c | 0.119b | 4.05b |
| 2.15 | 0.279d | 0.136b | 0.234d | 0.241a | 2.21c |
| Significant level | ** | ** | ** | ** | ** |

Different letters in each column show significant difference at $p \leq 0.01$ (**) by Least Significant Difference (LSD).

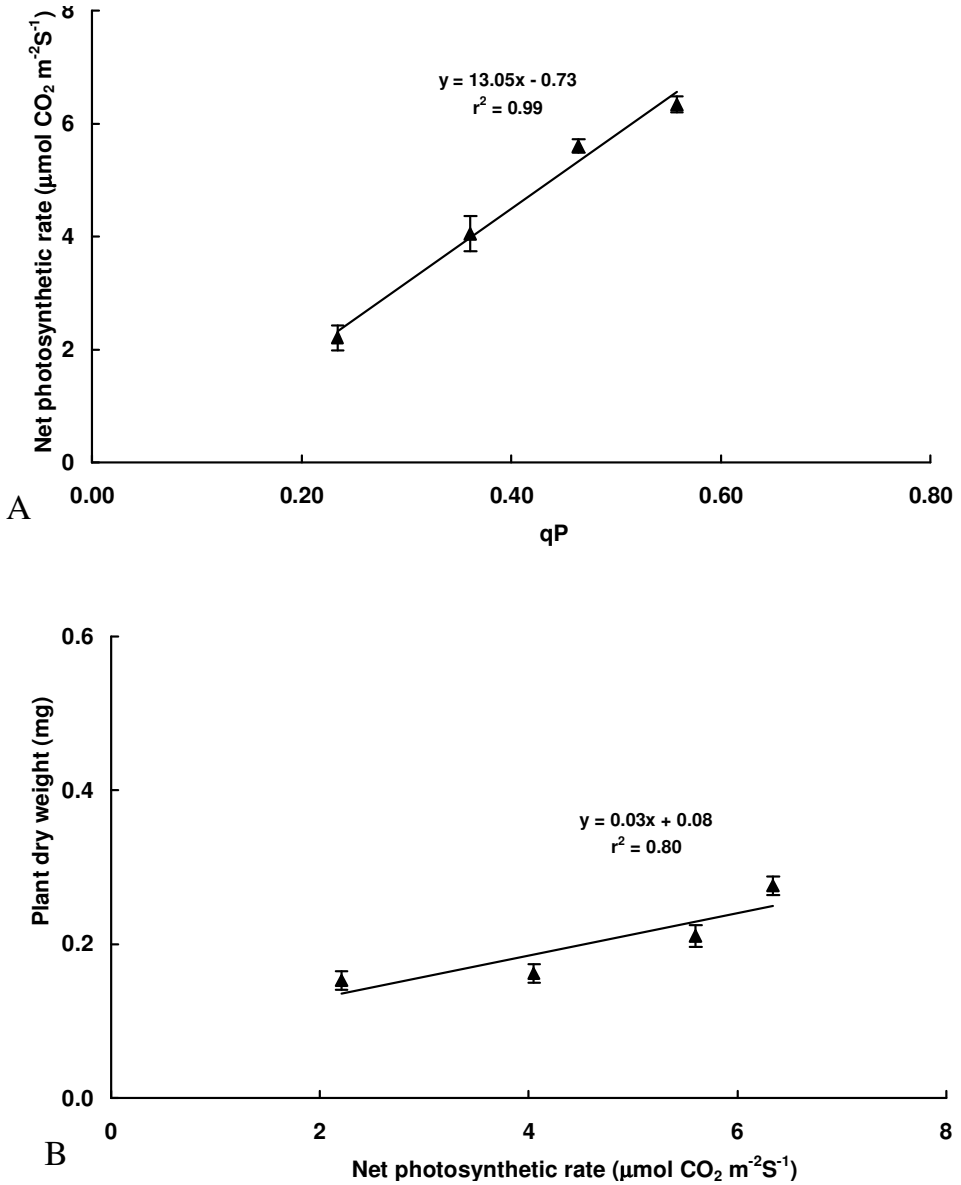


**Figure 4.** Relationship between quantum efficiency of PSII (qP) and net photosynthetic rate ($P_n$) (A) as well as $P_n$ and plant dry weight (B) of oil palm seedlings grown under PEG-induced water deficit for 14 days. Error bars are represented by ± SE.

**Table 3.** Relationship between physiological and biochemical parameters of oil palm seedlings grown under PEG-induced water deficit for 14 days.

| Parameter | $\Psi_s$ | $Chl_a$ | $Chl_b$ | $C_{x+c}$ | $F_v/F_m$ | $\Phi_{PSII}$ | qP | $P_n$ |
|---|---|---|---|---|---|---|---|---|
| $\Psi_s$ | - | - | - | - | - | - | - | - |
| $Chl_a$ | -0.933** | - | - | - | - | - | - | - |
| $Chl_b$ | -0.906** | 0.841** | - | - | - | - | - | - |
| $C_{x+c}$ | -0.870** | 0.922** | 0.896** | - | - | - | - | - |
| $F_v/F_m$ | -0.977** | 0.892** | 0.942** | 0.883** | - | - | - | - |
| $\Phi_{PSII}$ | -0.976** | 0.880** | 0.887** | 0.841** | 0.966** | - | - | - |
| qP | -0.962** | 0.821** | 0.948** | 0.847** | 0.972** | 0.947** | - | - |
| $P_n$ | -0.937** | 0.937** | 0.970** | 0.945** | 0.954** | 0.921** | 0.931** | - |

**Table 4** Growth characters, shoot height (SH), root length (RL), leaf area (LA), fresh weight (FW) and dry weight (DW) of oil palm seedlings grown under PEG-induced water deficit for 14 days.

| Osmotic potential (MPa) | SH (cm) | RL (cm) | LA ($cm^2$ $plant^{-1}$) | FW (g $plant^{-1}$) | DW (g $plant^{-1}$) |
|---|---|---|---|---|---|
| -0.24 (Control) | 23.1a | 12.0a | 49.0a | 1.25a | 0.28a |
| -0.42 | 20.6b | 8.5b | 38.5b | 0.84b | 0.21b |
| -0.98 | 18.8c | 5.5c | 25.7c | 0.55c | 0.16bc |
| -2.15 | 16.6d | 3.8c | 19.1d | 0.43c | 0.15c |
| Significant level | ** | ** | ** | ** | ** |

Different letters in each column show significant difference at $p \leq 0.01$ (**) by Least Significant Difference (LSD).

achieved by the plant's photosynthetic abilities which are inhibited by water deficit. The growth characters that is, SH, RL, LA, FW and DW, of oil palm seedlings were inhibited in response to PEG-induced water deficit. The inhibition of plant growth when subjected to water deficit conditions is demonstrated in date palm (Djibril et al., 2005).

In conclusion, osmotic potentials in PEG-induced water deficit of oil palm seedlings were decreased in both root and leaf tissues, leading to damage photosynthetic pigments and diminish photosynthetic abilities as well as reduce growth. The physiological and growth characters of oil palm seedlings decreased significantly, depending on the degree of water deficit.

## ACKNOWLEDGEMENTS

The authors are grateful to Jonathan Shore for grammatical proofing and Suksomboon Palm Co Ltd for providing oil palm seed. This experiment was funded by the National Center for Genetic Engineering and Biotechnology (BIOTEC) (Grant number BT-B-02-PG-BC-5102).

## Abbreviations

**PEG,** Polyethylene glycol; **$P_n$ ,** net photosynthetic rate; **RH,** relative humidity; **PPFD,** photosynthetic photon flux density; $Chl_a$, chlorophyll a; $Chl_b$, chlorophyll b; **TC,** total chlorophyll; **$C_{x+c}$,** total carotenoid; **$F_v$,** variable fluorescence yield; **PSII,** photosystem II; **$F_v/F_m$,** variable to maximum fluorescence; **NPQ,** non-photochemical quenching; **$C_{in}$,** carbon IV oxide inside; **$C_{out}$,** carbon IV oxide outside; **SH,** shoot height; **RL,** root length; **LA,** leaf area; **FW,** fresh weight; **DW,** dry weight; **$\Psi_s$,** osmotic potentials; **$F_v/F_m$,** maximum quantum yield of photosystem II; **$\Phi_{PSII}$,** photon yield of photosystem II; **qP,** quantum efficiency of photosystem II; **NPQ,** non photochemical quenching.

## REFERENCES

Ahmad S, Ahmad R, Ashraf MY, Ashraf M, Waraich EA (2009) Sunflower (*Helianthus annuus* L.) to drought stress at germination and seedling stages. Pak. J. Bot. 41: 647-654.

Bayoumi TY, Eid MH, Metwali EM (2008) Application of physiological and biochemical indices as a screening technique for drought tolerance in wheat genotypes. Afr. J. Biotechnol. 7: 2341-2352.

Blum A (2005). Drought resistance, water-use efficiency, and yield potential-are they compatible, dissonant, or mutually exclusive? Aust. J. Agric. Res. 56: 1159-1168.

Cattivelli L, Rizza F, Badeck FW, Mazzucotelli E, Mastrangelo AN, Francia E, Marè C, Tondelli A, Stanca AM (2008). Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. Field Crops Res. 105: 1-14.

Cha-um S, Mosaleeyanon K, Kirdmanee C, Supaibulwatana K (2003). A more efficient transplanting system for Thai neem (*Azadirachta*

*siamensis* Val.) by reducing relative humidity. Sci. Asia, 29: 189-196.
Chaves MM, Oliveira MM (2004). Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. J. Exp. Bot. 55: 2365-2384.
Cochard B, Amblard P, Durand-Gasselin T (2005). Oil palm genetic improvement and sustainable development. OCL 12: 141-147.
Cornic G (2000). Drought stress inhibits photosynthesis by decreasing stomatal aperture- not by affecting ATP synthesis. Trends Plant Sci. 5: 187-188.
Djibril S, Mohamed OK, Diaga D, Diégane D, Abaye FB, Maurice S, Alain B (2005). Growth and development of date palm (*Phoenix dactylifera* L.) seedlings under drought and salinity stresses. Afr. J. Biotechnol. 4: 968-972.
Fujiwara K, Kozai T, Watanabe I (1987). Fundamental studies on environment in plant tissue culture vessels. (3) Measurements of carbon dioxide gas concentration in closed vessels containing tissue cultured plantlets and estimates of net-photosynthetic rates of the plantlets. J. Agric. Method, 4: 21-30.
Gomes FP, Prado CHBA (2007). Ecophysiology of coconut palm under water stress. Braz. J. Plant Physiol. 19: 377-391.
Gomes FP, Oliva MA, Mielke MS, de Almeida AF, Leite HG, Aqino LA (2008). Photosynthetic limitations in the leaves of young Brazilian green dwarf coconut (*Cocos nucifera* L. 'nana') palm under well-watered conditions or recovering from drought stress. Environ. Exp. Bot. 62: 195-204.
Gopal J, Iwama K (2007). *In vitro* screening of potato against water-stress mediated through sorbitol and polyethylene glycol. Plant Cell Rep. 26: 693-700.
Henson IE, Harun MH (2005). The influence of climatic conditions on gas and energy exchanges above a young oil palm stand in north Kedah, Malaysia. J. Oil Palm Res. 17: 73-91.
Henson IE, Dolmat MT (2003). Physiological analysis of an oil palm density trial on a peat soil. J. Oil Palm Res. 15: 1-27.
Jalani BS, Cheah SC, Rajanaidu N, Darus A (1997). Improvement of palm oil through breeding and biotechnology. JAOCS, 74: 1451-1455.
Jone LH (1997). The effect of leaf pruning and other stresses on sex determination in the oil palm and their representation by a computer simulation. J. Theor. Biol. 187: 241-260.
Kallarackal J, Jeyakumar P, George SJ (2004). Water use of irrigated oil palm at three different arid locations in peninsular India. J. Oil Palm Res. 16: 45-53.
Kijne JW (2006). Abiotic stress and water scarcity: Identifying and resolving conflicts from plant level to global level. Field Crops Res. 97: 3-18.
Lanfermeijer FC, Koerselman-Kooij JW, Borstlap AC (1991). Osmosensitivity of sucrose uptake by immature pea cotyledons disappears during development. Plant Physiol. 95: 832-838.
Lichtenthaler HK (1987). Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. Methods Enzymol. 148: 350-380.
Loggini B, Scartazza A, Brugnoli E, Navari-Izzo F (1999). Antioxidant defense system, pigment composition, and photosynthetic efficiency in two wheat cultivars subjected to drought. Plant Physiol. 119: 1091-1099.
López R, Aranda I, Gil L (2009) Osmotic adjustment is a significant mechanism of drought resistance in *Pinus pinaster* and *Pinus canariensis*. Invest. Agra. Sist. Recur. Forest. 18: 159-166.
Maxwell K, Johnson GN (2000). Chlorophyll fluorescence-a practical guide. J. Exp. Bot. 51: 659-668.
Murashige T, Skoog F (1962). A revised medium for rapid growth and bioassays with tobacco tissue cultures. Physiol. Plant. 15: 473-479.
Nainanayake AD (2007). Use of chlorophyll fluorescence parameters to assess drought tolerance of coconut varieties. Cocos, 18: 77-105.
Neumann PM (2008). Coping mechanisms for crop plants in drought-prone environments. Ann. Bot. 101: 901-907.
Passioura J (2007). The drought environment: physical, biological and agricultural perspectives. J. Exp. Bot. 58: 113-117.
Reddy AR, Chaitanya KV, Vivekanandan M (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J. Plant Physiol. 161: 1189-1202.
Seki M, Umezawa T, Urano K, Shinozaki K (2007). Regulatory metabolic networks in drought stress responses. Curr. Opin. Plant Biol. 10: 296-302.
Shabala SN, Shabala SI, Martynenko AI, Babourina O, Newman IA (1998). Salinity effect on bioelectric activity, growth, $Na^+$ accumulation and chlorophyll fluorescence of maize leaves: a comparative survey and prospects for screening. Aust. J. Plant Physiol. 25: 609-616.
Valliyodan B, Nguyen HT (2006). Understanding regulatory networks and engineering for enhanced drought tolerance in plants. Curr. Opin. Plant Biol. 9: 189-195.
Wahid MB, Abdullah SNA, Henson IE (2005). Oil palm–Achievements and potential. Plant Prod. Sci. 8: 288-297.
Yordanov I, Velikova V, Tsonev T (2003). Plant responses to drought and stress tolerance. Bulg. J. Plant Physiol. 39: 187-206.
Yusof B, Chen KW (2003). Going back to basics: Producing high oil palm yields sustainably. Oil Palm Bull. 46: 1-14.