

IMPACTS OF WET AND DRY PERIODS ON LEAF GAS EXCHANGE, WATER USE EFFICIENCY AND CARBON ISOTOPE DISCRIMINATION IN DIFFERENT OIL PALM MATERIALS

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ABSTRACT

This study was conducted to investigate the effects of two different periods (i.e wet and dry) and five different oil palm materials [i.e. tenera (DxP) and clonal palms (i.e. PL68, PL104, PL106 and PL127)] on leaf carbon isotope discrimination (Δ), leaf gas exchange parameters such as net photosynthesis (P_N), stomatal conductance (g_s), transpiration rate (T_r), intercellular CO_2 concentration (c_i) and instantaneous water use efficiency (WUE) and their relationships, in different oil palm materials cultivated on peat. Leaf gas exchange of 8-year old DxP and clonal palms were determined during dry and wet periods which were also analysed for leaf Δ . Results showed that there were significant differences in P_N , g_s and T_r between different periods. The g_s values decreased by 54% during dry period compared to the wet period. This reduction in g_s led to a reduction of 59% and 44% in P_N and T_r , respectively. The interaction effect between oil palm materials and different periods had a significant influence on the leaf Δ values. Leaf Δ in clonal palm PL106 was less discriminated ($23.74 \pm 0.42\text{‰}$) compared to the DxP palm during dry season ($27.92 \pm 0.70\text{‰}$). A negative relationship was observed between leaf Δ with instantaneous WUE and leaf Δ was found to be highly correlated with c_i in oil palm during the wet period.

Keywords: leaf gas exchange, water use efficiency, carbon isotope discrimination.

Date received: 14 March 2018; **Sent for revision:** 16 March 2018; **Received in final form:** 17 July 2018; **Accepted:** 22 October 2018.

INTRODUCTION

Oil palm has become an increasingly attractive crop in the last few decades to meet the world's demand for oils and fats as it is able to produce up to 10 times more oil than in other oilseed crops in 1 ha of oil palm plantation (Lamade *et al.*, 2016). In Malaysia, the oil palm planted areas in 2016 reached 5.74 million hectares, an increase of only 1.74% against the 5.64 million hectares recorded in 2015, mainly due to the increase in new planted areas in Sarawak (Kushairi *et al.*, 2018).

The oil palm yield potential is affected when palms are exposed to stress conditions such as low moisture condition. The critical moisture stress periods for oil palm are 24 months, 18 months and five months prior to fruit maturation of the fruit bunches (Haniff *et al.*, 2010). If palms are subjected to water stress during the 24 months before fruit maturation, it will lead to a higher proportion of male inflorescences. Eighteen months before fruit maturation is the time of inflorescence abortion. If oil palm are subjected to water stress, fewer female inflorescence would be developed and smaller fruit bunches will be produced. Pollination is important in oil palm to ensure high fruitset and successful fruit bunch development. Pollination occurs five months before fruit maturity. If palms are

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subjected to heavy rainfall during pollination less pollination occurs and will affect the quality of fresh fruit bunches harvested (Haniff *et al.*, 2010). The increasing probability of seasonal droughts (Easterling *et al.*, 2000; Seneviratne *et al.*, 2010) and extreme rainfall emphasises the significance of traits such as water use efficiency (WUE) and drought tolerance fall under the selection criteria of oil palm production to alleviate the potential negative effects of future climate change (King *et al.*, 2013).

WUE is defined as plant dry matter production per unit of water loss through transpiration at the whole-plant level (Broeckx *et al.*, 2014). At the leaf level, instantaneous WUE of leaf gas exchange is the basic unit of production which could be moles of carbon gained in photosynthesis (P_N) in exchange for water used in transpiration (T_r) (Farquhar *et al.*, 1989). A similar parameter called intrinsic WUE, is defined as the ratio of P_n and stomatal conductance (g_s) (Erice *et al.*, 2007; Choi *et al.*, 2007; Ali and Talukder, 2008; Qiu *et al.*, 2008).

The P_N activity in the leaf is an integral process that depends on many biochemical reactions (Taiz and Zeiger, 2006). Water is an important factor for biochemical process in P_N . Stomatal closure is the primary diffusive limitation to P_N and one of the earliest responses to drought during the growing season (Wilson *et al.*, 2000; Chaves *et al.*, 2002; Flexas and Medrano, 2002). The P_N is inhibited during the dry period associated with the stomatal closure in oil palm under field condition due to changes in the saturation deficit of air and reduction in T_r (Dufrene and Saugier, 1993; Lamade and Setiyo, 1996; Bayona-Rodriguez *et al.*, 2016). Oil palm stomata will close early in the dry period and remain closed for a short period that can vary for several weeks depending on the level of drought severity (Villobos *et al.*, 1991). In the wet period, oil palm stomata open early in the morning and remain wide open throughout the day before closing in the early evening (Rees, 1961). A recent finding reported by Bayona-Rodriguez *et al.* (2016) found that a significant difference in photosynthetic behaviour among different measurement periods (*i.e.* dry, transition and wet) in oil palm under field condition in Columbia. Higher WUE indicates that plant uses the water efficiently for P_N . Many studies have been done to investigate the gas exchange and WUE of oil palm seedlings under water deficit and drought stress condition (Suresh *et al.*, 2010; Rivera *et al.*, 2012; 2016; Jazayeri *et al.*, 2015; Rivera *et al.*, 2016; Silva *et al.*, 2017). However, information on WUE of oil palm under field condition at different period is very limited. Previous studies reported that different species of oil palm respond differently to three different periods (*i.e.* wet, transition and dry). *E. guineensis* had a lower WUE during wet period than in dry period. However, WUE of interspecific

hybrid (*E. oleifera* × *E. guineensis*) was found to have no difference among periods (Bayona-Rodriguez *et al.*, 2016). Many research have been done to explore physiological traits that can be substitute to WUE measurement. The current measurement of WUE at the level could be determined using photosynthetic gas exchange but this method is laborious and unreliable method for long-term WUE (Johnson and Rumbaugh, 1995; Canavar *et al.*, 2014).

Carbon isotope composition ($\delta^{13}C$) of plant organic material varies among different types of plants and among plants grown in different environments (Nier and Gulbransen, 1939; Wickman, 1952). Discrimination against the naturally stable isotope ^{13}C occurs during photosynthetic CO_2 fixation and this is reflected in the $\delta^{13}C$ of plant tissue (Farquhar *et al.*, 1989). In C_3 plants, discrimination is largely dependent on the ratio between the concentration of CO_2 in the leaf intercellular space and that of ambient air (C_i/C_a) prevailing when the leaf carbon is assimilated. This ratio represents a balance between the rates of inward CO_2 diffusion controlled by stomatal conductance and CO_2 assimilation determined by photosynthesis (Farquhar *et al.*, 1982; 1989; Evans *et al.*, 1986).

Carbon isotope discrimination (Δ) could reduce time required for WUE measurement in plants. It has been used as an integrated measure of photosynthetic gas exchange to evaluate changes in environmental conditions. It also provides a long-term average estimate of C_i/C_a as a plant metabolism indicator (Farquhar *et al.*, 1982; 1989; Farquhar and Richard, 1984) and could be used as a comparative measure of instantaneous water use efficiency WUE and long-term transpiration efficiencies among species (Farquhar *et al.*, 1989). Carbon isotope discrimination (Δ) is a physiological trait that is related to WUE. The Δ is expected to be negatively correlated with WUE (Farquhar and Richards, 1984). Previous studies demonstrated that Δ value correlated with the WUE in *Coffea* species (Meinzer *et al.*, 1990; 1991) but no documentation on relationship between WUE and Δ of oil palm is reported.

The seasonal changes of P_N , T_r and WUE are important for plant production. Zona *et al.* (2012) reported that seasonal variability in P_N is a strong determinant of carbon-balance. Changes in climatic factors, such as rainfall and fluctuations in water availability, influence the yield of plants such as oil palm. Broeckx *et al.* (2014) suggested that the seasonal changes in Δ with P_N as a potential indicator of WUE provide a detailed field conditions of different water availability. However, information on gas exchange, instantaneous WUE and Δ in oil palm under different periods are limited. In this study, we evaluated the effects of periods and oil palm materials on leaf gas exchange, instantaneous WUE and Δ .

MATERIALS AND METHODS

Experimental Design and Planting Materials

The study was conducted at an oil palm plantation in Perak, Malaysia 101°05'22.248"E 3°49'09.167"N. Oil palm planting materials including commercial *tenera*, DxP and clonal palms (*i.e.* PL68, PL104, PL106, and PL127) were selected for this study. The oil palm planting materials were planted on shallow peat at a density of 136 palm ha⁻¹ in December 2007. Assessment was performed over four palms on each oil palm material between 17-26 November 2015 (wet period) and on 9-19 August 2016 (dry period). The monthly rainfall and number of rainy days in 2015 and 2016 are given in *Figure 1* and *Table 1*, respectively. The experiment was carried out in a randomised complete block design with two factors (*i.e.* planting material and period) and four replications. The oil palm was about 8-year old when the measurements were taken.

Leaf Gas Exchange Measurement

Leaf gas exchange parameters were measured on intact leaflets attached to frond 17 of oil palm materials with a portable photosynthesis system

(Model LI-6400XT, LI-COR, Inc., USA) together with the following benchmark parameters: 400 ppm CO₂ and 1000 μmol m⁻² s⁻¹ PAR radiation. Gas exchange parameters such as P_N , g_s , C_i and T_r rate were measured between 8:30 and 11:30 hr. Leaf temperature (T_l) is measured with a thermistor and instantaneous WUE was calculated as P_N/T_r . During the measurements, the ambient air temperature was 30.27°C and 30.51°C and leaf temperature was about 30.54°C and 31.11°C in the wet and dry periods, respectively. The ambient air humidity was 78.38% in the dry periods. However, air humidity data was not available in the wet period due to some other technical reason.

Chlorophyll Fluorescence Measurement

Chlorophyll fluorescence parameters were measured on intact leaflets attached to frond 17 of oil palm materials with Plant Efficiency Analyser (Pocket PEA, Hansatech, Instrument Ltd, England) for both measurement periods. Before measurement was done, oil palm leaflets were dark adapted for 15 min by attaching light-exclusion clips to the leaf surface then initial fluorescence (F_o), variable fluorescence (F_v), maximum fluorescence (F_m), efficiency of the water-splitting complex on the

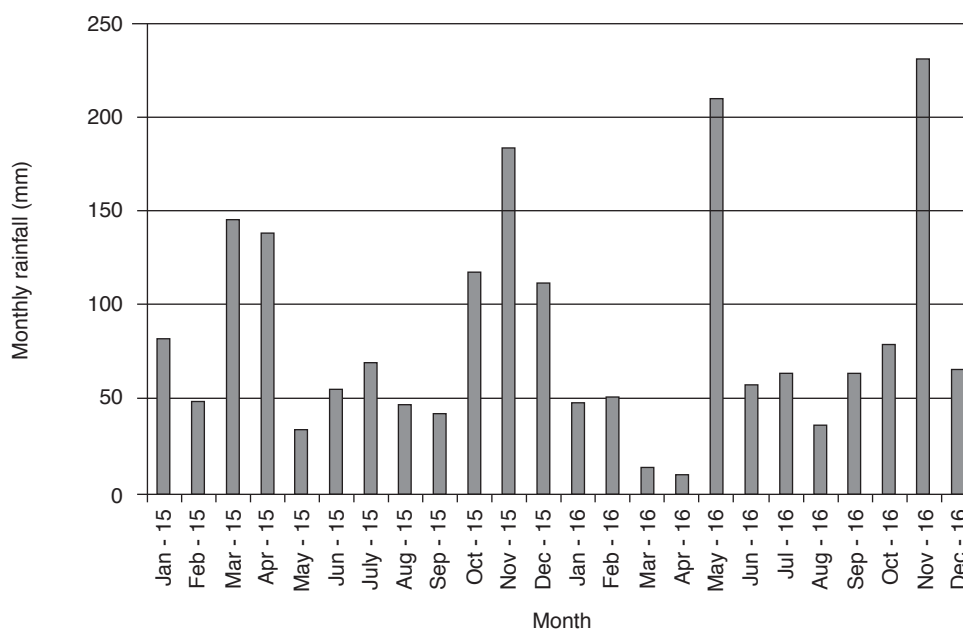


Figure 1. Monthly rainfall of oil palm plantation in Teluk Intan, Perak, Malaysia from January 2015 to December 2016.

TABLE 1. NO. OF RAINY DAYS AT OIL PALM PLANTATION IN TELUK INTAN, PERAK, MALAYSIA FROM JANUARY 2015 TO DECEMBER 2016

Year	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2015	7	1	14	18	5	4	5	7	8	14	17	12
2016	8	7	3	2	11	2	7	6	5	8	13	9

donor side of PSII (F_v/F_o), quantum yield of PSII (F_v/F_m) and performance index (PI) were determined.

Carbon Isotope Discrimination Determination

The ^{13}C was determined from the leaflets previously measured for leaf gas exchange. Leaf samples were oven dried at 70°C for 48 hr and ground to a fine powder. The relative abundance of ^{13}C and ^{12}C in the CO_2 produced in the leaf was determined using an Isotopic Ratio Mass Spectrometer at the Malaysian Institute of Nuclear Technology. Results were expressed as $\delta^{13}C$ (‰) using the equation given below (Farquhar *et al.*, 1989):

$$\delta^{13}C \text{ (‰)} = \left[\frac{R_p}{R_s} - 1 \right] \times 1000 \quad \text{Equation (1)}$$

where R_p is the $^{13}C/^{12}C$ ratio measured in the planting material and R_s is the $^{13}C/^{12}C$ ratio in the standard. The unit is expressed as part per thousand (‰). A secondary standard calibrated against Pee Dee Belemnite (PDB) carbonate was used for comparison. The following formula was used to calculate the leaf Δ value (Farquhar *et al.*, 1989):

$$\Delta \text{ (‰)} = \frac{\delta_a - \delta_p}{1 - \delta_p} \times 1000 \quad \text{Equation (2)}$$

where δ_p is the $\delta^{13}C$ of the sample and δ_a is the $\delta^{13}C$ of atmospheric CO_2 . On the PDB scale, atmospheric CO_2 has a current deviation of approximately -8‰ (Farquhar *et al.*, 1989).

Statistical Analysis

The data set was subjected to analyses of variance (ANOVA) and the differences between the means of treatments were compared using Duncan’s Multiple Range Test (DMRT) ($P \leq 0.05$). Pearson correlation analysis ($P \leq 0.05$) was performed to test the significance between the parameters. The entire data were processed using SAS software package 9 (SAS Institute, 2002).

RESULTS AND DISCUSSION

Rainfall distribution during wet and dry periods show that oil palm might be under soil water deficit coincided during dry period (Figure 1 and Table 1). From the present study, it was observed that the different periods had influenced the leaf gas exchange parameters such as P_N , g_s and T_r of oil palm ($P \leq 0.05$; Figures 2a to 2c). Photosynthetic rate ($19.63 \mu\text{mol m}^{-2} \text{s}^{-1}$), g_s ($0.34 \text{ mol m}^{-2} \text{s}^{-1}$) and T_r ($4.01 \text{ mmol m}^{-2} \text{s}^{-1}$) were statistically higher in the wet period compared to the dry period. Higher photosynthetic rate in oil palm during wet period associated with the higher in g_s and T_r might be due to higher soil water content. A relatively high amount of rainfall received before measurement time influenced the

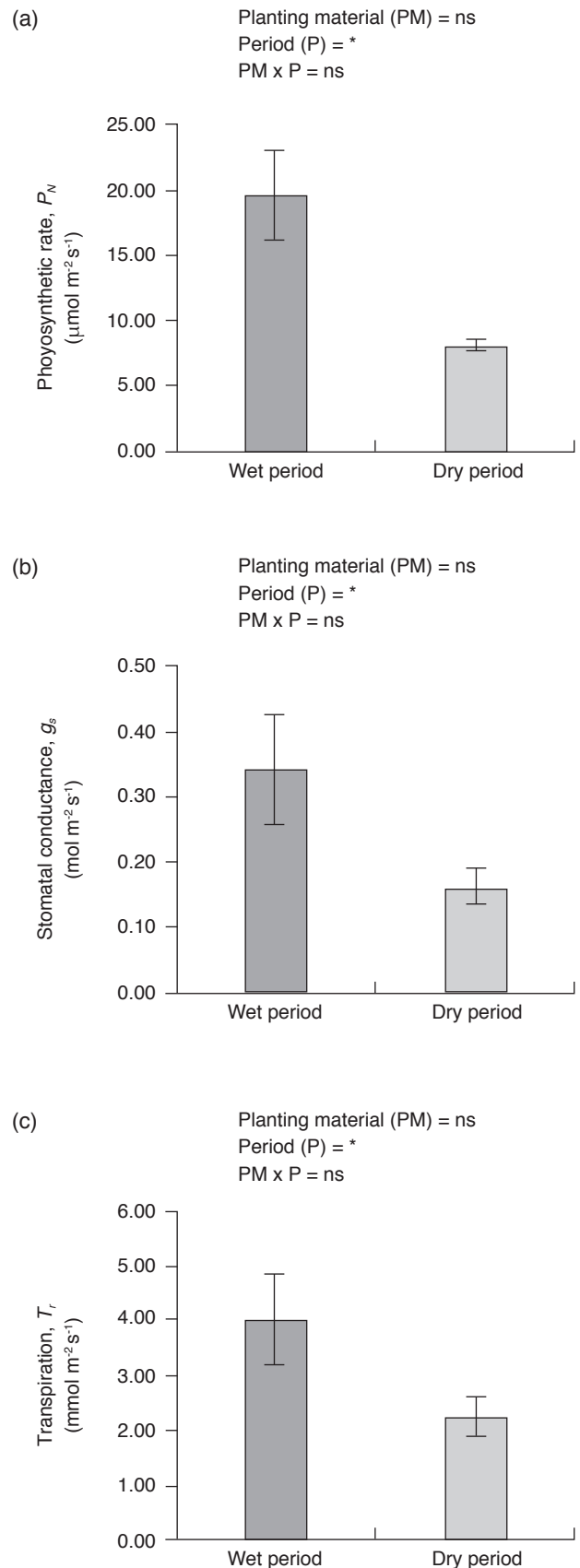


Figure 2. Photosynthetic rate (a), stomatal conductance (b) and transpiration rate (c) in oil palm cultivated on peat during wet and dry periods. Vertical bars represent \pm S.E of means of four replicates. * Significant at 5% level and ns = no significant ($P < 0.05$).

high CO_2 assimilation rate in oil palm. The g_s values dropped about 54% during the dry period compared to the wet period. This reduction in g_s led to a reduction of 59% and 44% in P_N and T_r , respectively. A similar finding was reported by Bayona-Rodriguez *et al.* (2016) on oil palm grown under rain fed conditions. They discovered that significant gas exchange differences were found among the seasons in the field with no irrigation and gas exchanges were lower during dry season compared to the dry-to-wet transition and wet seasons. Other studies also found similar results in nursery plants under water deficit, in *E. guineensis* progenies (Jazayeri *et al.*, 2015) and interspecific OxG hybrids (Rivera *et al.*, 2013). Henson and Haniff (2005) confirmed that during the dry period, the most immediate response is the stomatal closure and thus, the reduction of the T_r rates.

Leaf Δ was significantly influenced by interaction effects of periods and planting materials ($P \leq 0.05$; Figure 3). Results showed that leaf Δ in five oil palm planting materials did not respond in the same way during both wet and dry periods. Leaf Δ in DxP and clonal palms (*i.e.* PL68, PL194 and PL106) during wet period and were less discriminated compared to the dry period. Low in g_s and P_N had contributed to a relatively high leaf Δ values in oil palm materials during the dry period. This result is not in agreement with the other findings by Nunes *et al.* (2016) on eucalypt clones. They reported that lower leaf Δ in the eucalypt tolerant clone with lower g_s indicates a better stomata control while maintaining the photosynthetic rate for greater efficiency in the use of water. The differences between planting materials in leaf Δ was observed during the dry period. Results showed that there were variation in leaf Δ values of all oil palm planting materials during the dry period and DxP and clonal PL68 palms tend to increase the value of leaf Δ during the dry season. Leaf Δ was less discriminated in the clonal palm, PL106 (24.05‰)

compared to the DxP (27.92‰) palm during the dry season. The decrease in discrimination suggested that reduction in g_s resulted in limiting the P_N , which could be due to a decline in soil water. The decline in Δ was found when wheat seedlings were exposed to increasing levels of soil strength which decreased in soil water (Masle and Farquhar, 1988). In the present study, not all oil palm planting materials responded in the same way to drier soil conditions, indicating substantial genotypic variations in the degree of this response. Similar responses were observed in two *Coffea* species genotypes (Meinzer *et al.*, 1990).

Leaf Δ and instantaneous WUE in different oil palm materials were negatively correlated ($r = 0.65$, $P < 0.05$) (Table 2) during wet period. Therefore, leaf Δ values in oil palm is decreased when there is an increased in instantaneous WUE. Increased WUE is associated with a decrease in c_i as exhibited by a very significant correlation coefficient ($r = 0.99$, $P < 0.05$) (Table 2). At the same time, the decrease in leaf Δ of oil palm under wet period might be due to the decrease in c_i as exhibited by the significantly high value of correlation coefficient ($r = 0.64$, $P < 0.05$) (Table 2). This result indicates that lower in c_i could be a possible factor for lower in leaf Δ values in oil palm. Read and Farquhar (1991) also proposed that Δ is positively related to c_i . During dry period, no correlation was found between leaf Δ of oil palm material with leaf gas exchange and chlorophyll fluorescence parameters (Table 3). But increased in WUE of oil palm materials during dry period is associated with decrease in g_s , c_i and T_r (Table 3).

CONCLUSION

In conclusion, results showed that leaf gas exchange such as P_N , g_s and T_r rate in oil palm were significantly affected by wet and dry periods. The

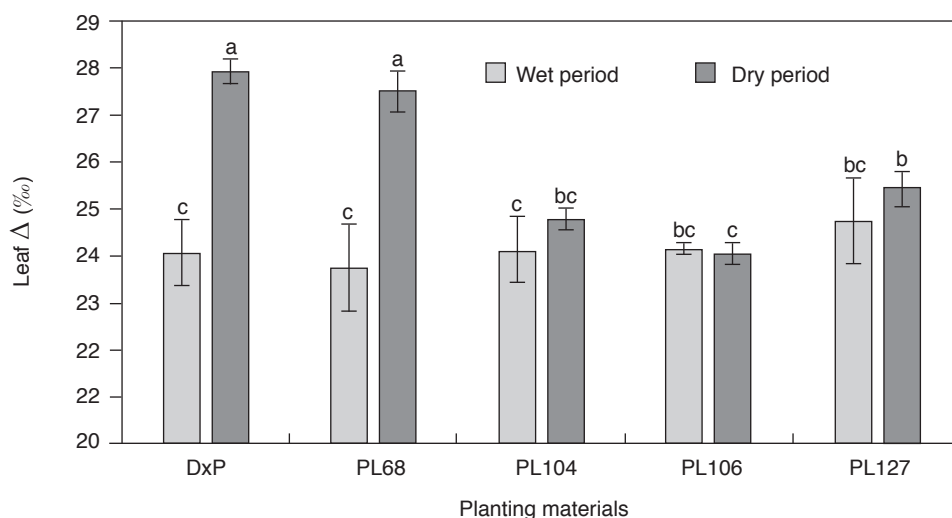


Figure 3. Interactive effects between periods and planting materials for leaf carbon isotope discrimination of oil palm. Vertical bars represent \pm S.E of means ($n=20$).

TABLE 2. CORRELATIONS BETWEEN LEAF CARBON ISOTOPE DISCRIMINATION (Δ), LEAF GAS EXCHANGE AND CHLOROPHYLL FLUORESCENCE PARAMETERS AS WELL AS LEAF TEMPERATURE AMONG FIVE OIL PALM MATERIALS DURING WET PERIOD

Parameters	P_N	g_s	c_i	T_r	WUE	Δ	F_o	F_m	F_v	F_v/F_o	F_v/F_m	PI	T_L
P_N	1.00	-	-	-	-	-	-	-	-	-	-	-	-
g_s	0.12	1.00	-	-	-	-	-	-	-	-	-	-	-
c_i	-0.60*	0.64*	1.00	-	-	-	-	-	-	-	-	-	-
T_r	0.11	0.97*	0.66*	1.00	-	-	-	-	-	-	-	-	-
WUE	0.64*	-0.60*	-0.99*	-0.64*	1.00	-	-	-	-	-	-	-	-
Δ	-0.29	0.53*	0.64*	0.63*	-0.65*	1.00	-	-	-	-	-	-	-
F_o	0.05	-0.04	-0.18	-0.01	0.15	0.02	1.00	-	-	-	-	-	-
F_m	-0.004	0.33	0.18	0.27	-0.15	0.12	0.46*	1.00	-	-	-	-	-
F_v	-0.02	0.36	0.23	0.30	-0.20	0.13	0.26	-0.98*	1.00	-	-	-	-
F_v/F_o	-0.05	0.27	0.31	0.22	-0.26	0.06	-0.54*	0.50*	0.66*	1.00	-	-	-
F_v/F_m	-0.04	0.35	0.35	0.31	-0.30	0.11	-0.50*	0.53*	0.69*	0.97*	1.00	-	-
PI	0.005	-0.10	0.23	0.08	-0.19	0.06	-0.75*	0.04	0.22	0.80*	0.70*	1.00	-
T_L	-0.06	-0.14	-0.12	-0.18	0.10	0.21	0.08	-0.31	-0.36	-0.37	-0.35	-0.21	1.00

Note: *Significant at $P \leq 0.05$, P_N - photosynthetic rate; g_s - stomatal conductance; c_i - intercellular CO_2 concentration; T_r - transpiration rate; WUE - instantaneous water use efficiency; Δ - leaf carbon isotope discrimination; F_o - initial fluorescence; F_m - maximum fluorescence; F_v - variable fluorescence; F_v/F_o - efficiency of the water-splitting complex on the donor side of PSII; F_v/F_m - quantum yield of PSII; PI - performance index and T_L - leaf temperature, *Significant at 5% level.

TABLE 3. CORRELATIONS BETWEEN LEAF CARBON ISOTOPE DISCRIMINATION (Δ), LEAF GAS EXCHANGE AND CHLOROPHYLL FLUORESCENCE PARAMETERS AS WELL AS LEAF TEMPERATURE AMONG FIVE OIL PALM MATERIALS DURING DRY PERIOD

Parameters	P_N	g_s	c_i	T_r	WUE	Δ	F_o	F_m	F_v	F_v/F_o	F_v/F_m	PI	T_L
P_N	1.00	-	-	-	-	-	-	-	-	-	-	-	-
g_s	0.64*	1.00	-	-	-	-	-	-	-	-	-	-	-
c_i	0.10	0.73*	1.00	-	-	-	-	-	-	-	-	-	-
T_r	0.72*	0.98*	0.70*	1.00	-	-	-	-	-	-	-	-	-
WUE	0.002	-0.70*	-0.98*	-0.65*	1.00	-	-	-	-	-	-	-	-
Δ	-0.02	0.01	0.08	0.08	-0.11	1.00	-	-	-	-	-	-	-
F_o	-0.36	-0.21	-0.11	-0.29	0.06	-0.21	1.00	-	-	-	-	-	-
F_m	-0.23	-0.29	-0.20	-0.33	0.20	-0.21	0.77*	1.00	-	-	-	-	-
F_v	-0.20	-0.29	-0.21	-0.32	0.22	-0.19	0.69*	0.99*	1.00	-	-	-	-
F_v/F_o	0.14	-0.14	-0.14	-0.11	0.22	-0.04	-0.19	0.46*	0.57*	1.00	-	-	-
F_v/F_m	0.16	-0.15	-0.15	-0.10	0.22	0.003	-0.23	0.43	0.54*	0.99*	1.00	-	-
PI	0.18	-0.09	-0.17	-0.04	0.21	0.17	-0.72	-0.24	-0.13	0.66*	0.67*	1.00	-
T_L	-0.16	-0.24	-0.004	-0.23	0.06	-0.21	0.07	-0.05	-0.07	-0.12	-0.13	-0.01	1.00

Note: *Significant at $P \leq 0.05$. P_N - photosynthetic rate; g_s - stomatal conductance; c_i - intercellular CO_2 concentration; T_r - transpiration rate; WUE - instantaneous water use efficiency; Δ - leaf carbon isotope discrimination; F_o - initial fluorescence; F_m - maximum fluorescence; F_v - variable fluorescence; F_v/F_o - efficiency of the water-splitting complex on the donor side of PSII; F_v/F_m - quantum yield of PSII; PI - performance index and T_L - leaf temperature, *Significant at 5% level.

decline in leaf gas exchange in oil palm was more prominent during the dry period. The interaction effects between different periods and oil palm planting materials significantly affected the leaf Δ . Leaf Δ is negatively correlated with instantaneous WUE during wet period and influenced by the intercellular CO_2 concentration. We conclude that leaf Δ could be used as a rapid tool for assessing plant performance since it responded to different environment conditions. Further comprehensive studies on the seasonal leaf Δ of oil palm as well as during wet, transition and dry season are required to

clarify the usefulness of leaf Δ as a substitute trait for evaluating plant response at various environmental conditions.

ACKNOWLEDGEMENT

We wish to thank the Director-General of MPOB for permission to publish this article. We also would like to thank the staff of Crop Physiology Group and Breeding and Tissue Culture Unit of Advanced Biotechnology and Breeding Centre, MPOB for their technical assistance and expertise in this project.

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