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Gas-exchange characteristics, leaf water potential and chlorophyll *a* fluorescence in oil palm (*Elaeis guineensis* Jacq.) seedlings under water stress and recovery

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Abstract

The gas-exchange characteristics, leaf water potential and chlorophyll (Chl) *a* fluorescence of oil palm (*Elaeis guineensis* Jacq.) seedlings subjected to water stress and recovery were investigated in a greenhouse experiment. At 24 days after imposition of stress, leaf water potential in water-stressed seedlings was doubled compared to that of control and there was a drastic decline in gas-exchange parameters *viz*. photosynthesis, transpiration, and stomatal conductance. Water stress did not irreversibly affect gas-exchange parameters and quantum efficiency of photosystem II, as seedlings exhibited total recovery of photosynthetic apparatus by 12th day of rehydration. These findings indicate that oil palm exhibits physiological plasticity to water stress during the seedling stage.

Additional key words: Elaeis guineensis, photosynthesis, photosystem II, stomatal conductance, transpiration.

Introduction

Oil palm (*Elaeis guineensis* Jacq.), a high-oil-yielding crop has been introduced in India to meet the vegetable oil demand by its huge population. Accordingly, an area of about 8 ha was identified in various provinces of India. Irrigation is considered to be one of the important factors for realizing better yields as water deficit not only leads to reduced growth but also affects plant physiology. Water stress during growth of oil palm not only causes a general reduction in size but also exhibits characteristic modifications in structure, particularly leaves with reduced area. In such cases, stomata close early and gaseous exchange between plant and atmosphere reduces considerably leading to decreased yields (Rees 1961, Corley *et al*. 1973, Suresh and Nagamani 2006). There is a big controversy as to whether water deficits mainly limit photosynthesis by stomatal closure (Flexas *et al*. 2006) or metabolic damage (Lawlor and Cornic 2002). Stomatal regulation in oil palm is particularly delicate and enables plant to minimize water losses in an event of water stress. Reduction in stomatal conductance is one of the initial responses used by plants during water stress for decreasing transpiration and turgor maintenance (Eckstein and Robison 1996), while transpiration loss becomes less due to stomatal closure, it also reduces photosynthesis (de Souza *et al*. 2001). The net photosynthetic rate and stomatal conductance of attached leaves of sunflower decreased as leaf water potential declined (Tezara *et al*. 2008).

The response of photosynthesis to water stress is important as water is an electron donor that allows maintenance of this process. Water stress also induces alterations in photochemical reactions resulting in stomatal and nonstomatal limitations with damage to reaction centers of photosystem I and II (PSI and PSII) (Angelopoulos *et al*. 1996). The fluorescence of water-stressed barley plants was characterized by a mild decrease of F_v/F_p (where F_v is variable part of Chl fluorescence and F_p is Chl fluorescence intensity at peak

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Abbreviations: C_a – ambient CO_2 concentration; Chl – chlorophyll; E – transpiration rate; ETR – apparent rate of photochemical transport of electrons through PSII; F_m – maximum fluorescence; F_m' – maximum fluorescence yield acclimated to irradiation; F_o – minimal fluorescence; F_0' – initial fluorescence in leaves acclimated to irradiation; F_p – Chl fluorescence intensity at peak of continuous fluorescence inductive curve; F_s – steady state fluorescence in leaves acclimated to irradiation; F_v – variable part of Chl fluorescence; F_v/F_m – photochemical efficiency of photosytem II; g_s – stomatal conductance; NPQ – coefficient of non-photochemical quenching of excitation energy; *Ndh* – nicotinamide adenine dinucleotide (phosphate) dehydrogenase; PAR – incident photosynthetically active radiation in leaf; P_N – net photosynthetic rate; PSI – photosystem I; PSII – photosystem II; Q_A – quinone A; q_L – coefficient of photochemical quenching; WUE – water-use efficiency; Ψ_w – leaf water potential; Φ_{PSII} – effective quantum yield of PSII.

of continuous fluorescence inductive curve) and significant increase of F_0 (Chl fluorescence with all PSII reaction centres open), together with a slight decrease of F_p (Matoušková *et al.* 1996). As information on effect of water stress on oil palm seedlings and its rehydration (recovery) is scarce, the present study was taken up to understand gas-exchange characteristics, leaf water potential and Chl *a* fluorescence in oil palm seedlings.

Materials and methods

The study was conducted at Directorate of Oil Palm Research, Pedavegi, which is situated in West Godavari district of Andhra Pradesh province in India. The experimental site (Pedavegi) is located at 16° 43'N and 81° 09'E with a mean sea level of 13.41 m. The average rainfall is 1,221 mm. Oil palm seedlings (*tenera* hybrid) which are approximately 10 months old were , selected according to their uniformity in size. The plants were grown in plastic bags (size 45 × 50 cm) containing a mixture of sand, soil, and farm yard manure (1:3:1, v/v/v) and subjected to a period of 30 days of acclimatization to light and temperature under greenhouse conditions [mean temperature: 26/19°C (day/night), relative humidity: 75–85%, photon flux density: 700–800 μmol m^{-2} s^{-1}). During this period, all bags were irrigated daily to maintain field capacity. The field capacity was considered to be reached when water percolated through the bag to ground under it and the soil was saturated. After acclimatization, plants were separated into two groups of 20 plants each. One group continued to receive daily irrigation which was control and other was induced to water stress by withholding irrigation. Gas-exchange parameters, leaf water potential and Chl *a* fluorescence were measured at every 4th day throughout the study. At 24th day, when photosynthetic rate was close to zero, it was assumed that stomatal closure had occurred and water-stressed seedlings were rewatered. Since recovery process in terms of gas-exchange parameters was slow, data are presented at 4-day intervals after rehydration for convenience.

Gas-exchange measurements like net photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration (E) were recorded using a portable photosynthesis system (*LCA-4, ADC*, Hertfordshire, UK) connected to a *PLC 4* (6.25 cm^2) leaf chamber. During measurements, incident photon flux density was 800 μmol(photon) m^{-2} s^{-1}, leaf temperature 25°C and ambient CO_2 concentration (C_a) 360 μmol mol^{-1}. The measurements were made on a fully opened healthy leaf (3rd leaf from top) under bright sunlight between 10:00 and 11:00 h. Water-use efficiency (WUE) was determined by the ratio of P_N to E.

Leaf water potential (Ψ_w) was measured at every 4th day after initiation of water stress and subsequent rehydration. Leaf discs (6 mm in diameter) were sampled and placed in a *C-52-SF* sample chamber (*Wescor Inc*., Logan, UT, USA). The samples were allowed to equilibrate and then measured with dew point microvoltmeter (*Model HR-33T, Wescor Inc*., Logan, UT, USA). Five leaf samples from a fully opened healthy leaf (3rd leaf from the top) were taken at each sampling. All observations were made between 10:00 and 11:00 h.

Chl *a* fluorescence parameters were measured using photosynthesis yield analyzer (*Mini-Pam, Walz*, Effeltrich, Germany). The minimal fluorescence (F_0) was measured in 30-min-dark-adapted leaves using weak modulated irradiance (<0.1 μmol m^{-2} s^{-1}). A 600-ms saturating flash (>7,000 μmol m^{-2} s^{-1}) was applied to determine the maximum fluorescence (F_m) and photochemical efficiency of photosytem II (PSII) (F_v/F_m). Then the leaves were continuously irradiated with white actinic light (600 μmol m^{-2} s^{-1}) in order to measure the steady-state fluorescence yield (F_s) and maximum fluorescence yield (F'_m) of irradiated leaves. The following Chl *a* fluorescence parameters were calculated: maximum quantum efficiency of PSII primary photochemistry (F_v/F_m), as per van Kooten and Snel (1990); effective quantum yield of PSII [$\Phi_{PSII} = (F_m' - F_s)/F_m'$], according to Genty *et al.* (1989); apparent rate of photochemical transport of electrons through PSII [$ETR = \Phi_{PSII} \times PAR \times 0.5 \times 0.84$], as per Schultz (1996). The coefficient of photochemical quenching (according to the lake model) [$q_L = (F_m' - F_s)\, F_0'/(F_m' - F_0')\, F_s$] was determined as per Kramer *et al.* (2004) and the coefficient of non-photochemical quenching of excitation energy [$NPQ = (F_m - F_m')/F_m'$] according to Schreiber *et al.* (1994), where F_0 – initial fluorescence in leaves subjected to dark; F_m – maximum fluorescence in leaves acclimated to dark; F_v = variable fluorescence in leaves acclimated to dark [$F_v = F_m - F_0$]; F_0' – initial fluorescence in leaves acclimated to irradiation; F_m' – maximum fluorescence in leaves acclimated to irradiation; F_s – steady state fluorescence in leaves acclimated to irradiation; PAR – incident photosynthetically active radiation in leaf; 0.5 corresponds to the proportion of absorbed quanta used by PSII reaction centres; and 0.84 represents the proportion of incident irradiance absorbed by leaf. F_0' has been calculated by the instrument software.

Experimental design and statistical analysis: The experimental design was completely randomized with two treatments (irrigation and water stress) and twenty replicates. Each plant (seedling) was considered as a replication. Statistical analysis was done using *MSTAT* statistical software (*MSTAT,* developed by Dr. Russel Freed, Crop and Soil Sciences Department of Michigan State University, USA). Data was subjected to analysis of variance (*ANOVA*). *Tukey* test ($p<0.05$) was used to compare means among treatments.

Results and discussion

Ψ_w and gas-exchange parameters after imposition of stress: Ψ_w in oil palm seedlings showed significant differences between two treatments on 12th day after imposition of water stress. The Ψ_w was –3.6 MPa at 24th day after imposition of stress, which was associated with P_N of 0.05 µmol m^{-2} s^{-1} due to stomatal closure (Fig. 1). Similar findings were reported in tree species like *Stryphinodendron adstringens* (Rocha and Moraes 1997) and *Malphighia emarginata* (Nogueira *et al.* 2001), where P_N was close to zero, when the Ψ_w values were approximately –2.7 MPa and between –4.5 to –5.3 MPa respectively. In sunflower also, P_N and g_s decreased as leaf water potential declined from –0.3 to –2.9 MPa (Tezara *et al.* 2008).

The P_N at the start of experiment was 6.10 µmol m^{-2} s^{-1} and progressively decreased to 0.05 µmol m^{-2} s^{-1} at 24 days after imposition of water stress. Stomatal conductance (g_s) was significantly reduced from 8th day onwards after imposition of stress. The stomatal closure occurred at 24th day after imposition of water stress in water-stress treatment and consequently reached values close to zero. Though P_N and g_s declined due to water stress, mesophyll conductance (not studied here) also plays an important role in ascertaining the exact relationship. Dufrene *et al.* (1992) found that g_s in oil palm declined when the fraction of available water in top 80 cm of soil fell to 0.67 equivalent to soil water deficit of 24 mm. Ni and Pallardy (1992) and Flexas *et al.* 2006 have reported that plants show a decline in g_s and P_N with the increased water stress.

E at start of the study was 0.13 mmol m^{-2} s^{-1} which progressively declined to 0.01 mmol m^{-2} s^{-1} at 24th day after imposition of water stress. *E* decreased to more than 50% in water-stressed seedlings at 12th day after imposition of stress. This sort of controlled transpiration has been reported in many woody species of *Rapanea guianensis* (Naves-Barbiera *et al.* 2000), vine seedlings (de Souza *et al.* 2001), *Tubebura aurea* plants (Silva *et al.* 2003) and *Acariquara* seedlings (Liberato *et al.* 2006), which restrict water loss to overcome periods of water

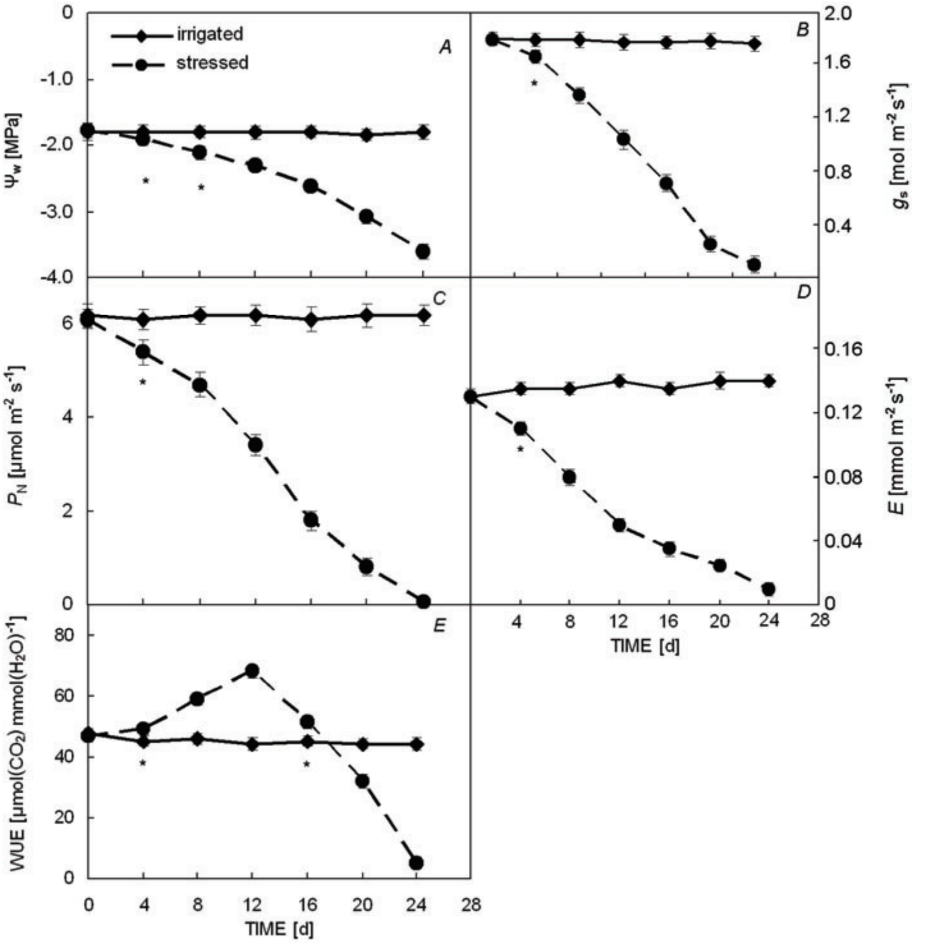

Fig. 1. Leaf water potential (Ψ_w), stomatal conductance (g_s), net photosynthetic rate (P_N), transpiration rate (E) and water-use efficiency (WUE) in oil palm seedlings under irrigated and water-stress treatments. Mean values indicated by * are not significantly different at $p<0.05$. *Vertical bars* represent SE for $n = 20$.

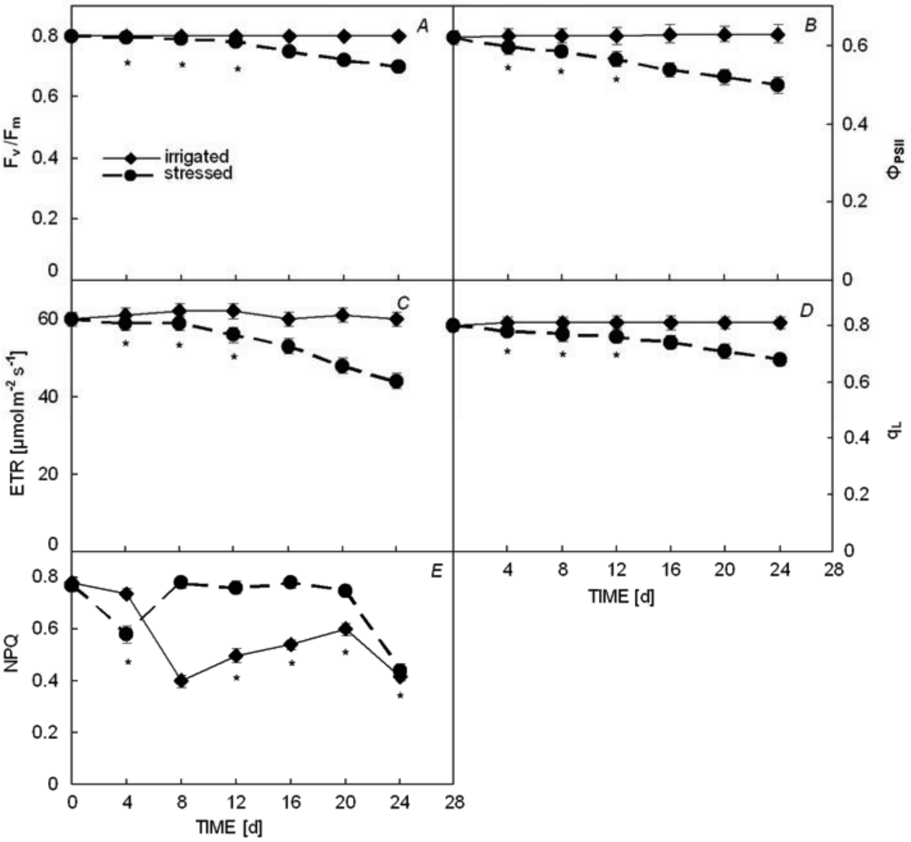

Fig. 2. Maximum quantum efficiency of PSII primary photochemistry (F_v/F_m), effective quantum yield of PSII (Φ_{PSII}), apparent photochemical electron transport rate (ETR), photochemical quenching of excitation energy (q_L) and non-photochemical quenching of excitation energy (NPQ) in oil palm seedlings under irrigated and water-stress treatments. Mean values indicated by * are not significantly different at $p<0.05$. *Vertical bars* represent SE for $n = 20$.

stress. WUE in water-stressed oil palm seedlings was greater than that of control till 16th day and declined sharply thereafter. WUE was increased due to reduced g_s, which led to greater decline in E than P_N. Similar findings were reported by Rocha and Moraes (1997) in *Styphnodendron adstringens*.

Chl *a* fluorescence after imposition of stress: F_v/F_m dropped to 0.7 in the oil palm seedlings at 24th day after imposition of water stress (Fig. 2). Similarly Φ_{PSII}, q_L, and ETR were 0.5, 0.68, and 44 µmol m^{-2} s^{-1}, respectively, at 24th day in water-stressed seedlings. In barley plants also, fluorescence was characterized by a mild decrease of F_v/F_p (Matoušková *et al.* 1996). A linear reduction in coefficient of photochemical quenching with decreasing relative water content was reported by da Silva and Arrabaca (2004). The decrease in F_v/F_m ratio under water stress can be ascribed to the inactivity of PSII reaction centres, which is mainly due to degradation of D1 and D2 proteins responsible for transfer of water electrons to Chl *a* associated with PSII reaction centres (Hao *et al.* 1999, Lazár 1999). The progressive decline in Φ_{PSII} and ETR after 30 days without irrigation might be due to inability of plastoquinone complexes (responsible for photochemical transport of electrons between photosystem I and II) to carry out oxido-reduction reactions. The proportion of electrons transported from PSII and stomatal opening for photosynthesis are related to q_L. The decrease in q_L values indicated an increase in quinone A (Q_A) in reduced state, which occurred due to increased proportion of inactive PSII reaction centres (Quick and Horton 1984, Dietz *et al.*1985, Genty *et al.* 1989). The behaviour of gas-exchange parameters and electron transport in oil palm seedlings subjected to water stress could be due to the decreased rate of photochemical quenching of the excitation energy.

During water stress, plants can activate the protective mechanism of PSII which dissipates excess excitation energy through non-photochemical quenching (Casper *et al.* 1993). Though both the processes of photochemical and non-photochemical quenching of excitation of energy are competitive, an increase in one causes the decrease of the other (Krause and Weis 1991). However such responses did not occur in oil palm seedlings subjected to water stress. The non-photochemical quenching of excitation energy (NPQ) was not significantly different among seedlings in control and water stress during 24-d period. These findings might be due to light protection

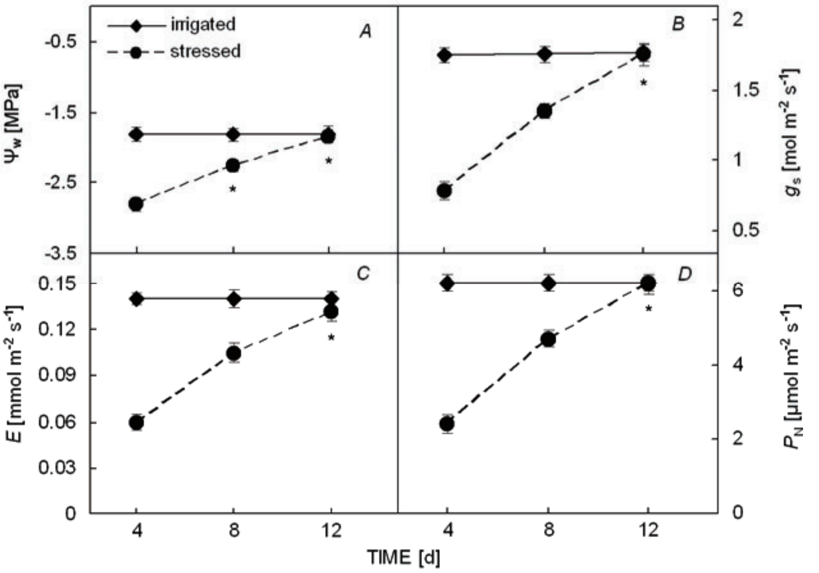

Fig. 3. Effect of rehydration on leaf water potential (Ψ_w), stomatal conductance (g_s), transpiration (*E*), and net photosynthetic rate (P_N) in oil palm seedlings. Mean values indicated by * are not significantly different at $p<0.05$. *Vertical bars* represent SE for $n = 20$.

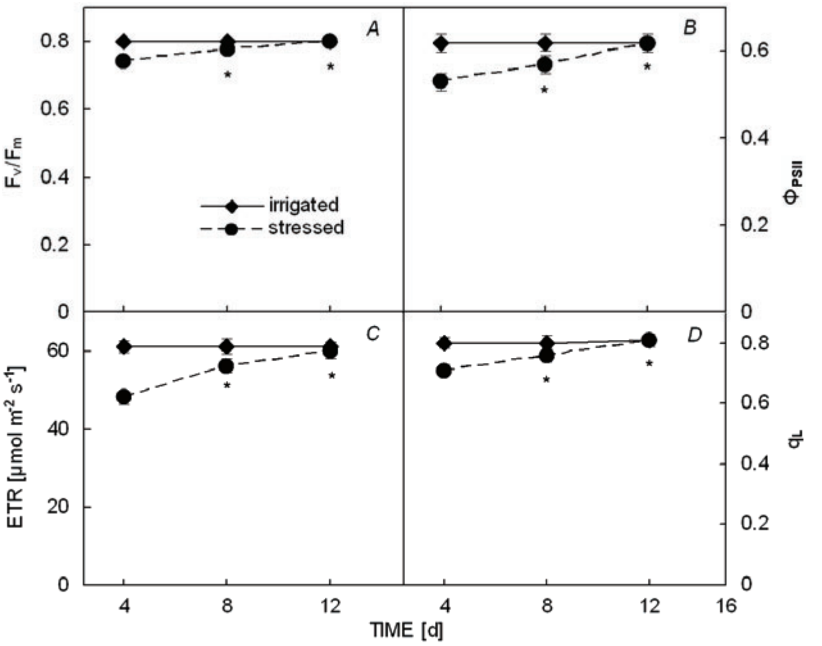

Fig. 4. Effect of rehydration on maximum quantum efficiency of PSII primary photochemistry (F_v/F_m), effective quantum yield of PSII (Φ_{PSII}), apparent photochemical electron transport rate (ETR), and photochemical quenching of excitation energy (q_L) in oil palm seedlings. Mean values indicated by * are not significantly different at $p<0.05$. *Vertical bars* represent SE for $n = 20$.

activity of nicotinamide adenine dinucleotide (phosphate) dehydrogenase (*Ndh*), a component of respiratory electron transport, present in chloroplast thylakoid membrane (Bennoun 2002). The *Ndh* complex oxidizes stromal reductant in presence of light and avoids generation of reactive oxygen species in stroma, thereby acting as an emergency electron sink in photosynthetic electron transport.

Ψ_w and gas-exchange parameters after stress recovery: The Ψ_w in water-stressed oil palm seedlings recovered from –3.6 MPa at 24th day after water stress to –2.8 MPa at 4th day after rehydration and reached similar value to that of control at 12th day after rehydration (Fig. 3). P_N, g_s, and *E* also followed similar trend as that of Ψ_w in stressed oil palm seedlings after rehydration. The gas-exchange parameters were not significantly different among oil palm seedlings (control and rehydration) at 12th day after rehydration, which indicates that oil palm seedlings took 12 days to recover from water stress given for 24 days. These findings probably reveal that mesophyll cells are not irreversibly affected by water stress due to the fact that a gradual recovery of these parameters is happening after resumption of irrigation. Similar findings have been reported by different workers though the period of recovery varied with species. Calbo and Moraes (1997) observed that young *Maurina vinifera* plants maintained without irrigation for 41 days showed total recovery of photosynthesis 5 days after rehydration. While in *Eutrepe* *oleraceae* plants without irrigation for 61 days, the period of recuperation of gas-exchange parameters was 14 days after irrigation (Calbo and Moraes 2000).

Chl *a* fluorescence after stress recovery: F_v/F_m in water-stressed oil palm seedlings was on par with control at 12th day after rehydration (Fig. 4). The differences in Φ_{PSII} and ETR values were not significant at 8th day after rehydration between control and water-stressed seedlings. It indicates that Mehler's reaction and photorespiration could have played an important role in reestablishment of flux of electrons from 8th day of rehydration process. Also differences in q_L values were not significant between control and stressed seedlings after 8th days of rehydration.

The above findings indicate that oil palm seedlings tolerated water stress by regulating g_s (though mesophyll conductance also played a vital role) which in turn helped in maintaining positive values of photosynthetic rates with reduced stomatal opening along with lower Ψ_w. The decline in F_v/F_m during water stress may be related to the activation of protection mechanisms in oil palm seedlings as rehydrated seedlings recovered their photosynthetic activity. The results also show that oil palm seedlings posses physiological plasticity during water stress and its subsequent recovery after rehydration.

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There is no doubt that English has become the most important world-wide language used in scientific communication. On the other side, the number of non-native English speakers publishing in scientific journals has rapidly increased recently, which is probably connected with a huge economic development especially in Asia and the countries of the so-called third world.

As the amount of scientific findings is constantly arising, there is a need to communicate research results in as concise form as possible. This may be a serious problem not only for English speakers but all the more for non-native ones.

The goal of the presented book is to help especially to non-native English speakers write their research papers for publication in English. But even native speakers may find useful information here since not every good scientist is also a good writer. The book deals not only with vocabulary and grammar which is typical for science research papers but offers also a comprehensive overview about the most common structure of a paper with specific needs of its single parts.

The book is divided into five units, each of them dealing with one chapter of the paper (Introduction, Methodology, Results, Discussion/Conclusion, Abstract). Every unit has a similar structure, which enables a reader to orientate himself very easy in the text. First an example of the chapter is given, then grammar and writing skills causing usually problems are discussed. After that the reader is invited to create a model for writing of that chapter (*e.g.* Introduction) and use it for his own example chapters. A rich vocabulary with most frequently used nouns, adjectives, verbs and phrases is connected. At the end of the unit the reader can try to write his own chapter and compare it with a sample answer.

At the end of the book, four useful Appendices are presented: Latin abbreviations, prefixes, Latin and Greek singular and plural forms, and useful verbs used in science writing.

Very well written and user-friendly book is suitable for all researchers, students, industrial scientists and the other who publish their findings in English science journals and are interested in the best possible readibility, and language and style accuracy of their papers. The book is intended for those whose English language proficiency is at intermediate level or above. Since the book responds to a lot of frequently-asked questions regarding science writing, it should not be certainly missing in any laboratory and/or academic library.

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