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BRIEF COMMUNICATION

The effect of phyllode temperature on gas exchange and chlorophyll fluorescence of *Acacia mangium*

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Abstract

The optimum temperature for photosynthetic CO_2 assimilation of *A. mangium* phyllodes was 30-32 °C. Photosystem 2 (PS 2) exhibited high tolerance to high temperature. Gas exchange and the function of PS2 of *A. mangium* were adapted to the temperature regime of the tropical environment and this might be the contributing factor to their fast growth under tropical conditions.

Additional key words: dark respiration rate; net photosynthetic rate; photochemical and non-photochemical quenching; photosystem 2 efficiency; stomatal conductance; transpiration rate.

The response of plant growth to temperature is directly related to the photosynthetic response to temperature (Pastenes and Horton 1999). In order to predict carbon sequestration by vegetation with the future rise in atmospheric temperature, the effects of high temperatures on the photosynthetic responses of plants need to be elucidated. However, the response of photosynthetic capacity of trees to temperature has seldom been studied (Dreyer *et al.* 2001).

Acacia mangium Willd. is a tropical pioneer tree species that is widely used in reforestation and pulp wood plantations (Sim 1986, Mok *et al.* 2000). Its photosynthetic parameters strongly depend on growth irradiance (Yu 2002). *A. mangium* develops two distinctive leaf types during its life history. During the juvenile phase (eight weeks after sowing), it produces true compound leaves, which are later replaced by phyllodes (expanded petioles that form simple, photosynthesising laminae in older plants; see Atkins *et al.* 1998). The aim of the present paper was the study of the effects of high temperature on photosynthesis of *A. mangium* plants and the underlying ecophysiological mechanisms that contribute to its fast growth in high temperature tropical environments.

Three to four *A. mangium* seedlings were grown in a plastic pot (diameter 33 cm, height 26 cm) filled with vermiculite, in an open-sunny site, under natural conditions, in the teaching garden of National University of Singapore. Experiments on the changes in gas exchange characteristics and Chl fluorescence parameters of *A. mangium* phyllodes in response to different phyllode temperatures were conducted with 250-d-old plants. Determinations of photon-saturated net photosynthetic rate (P_N) in attached mature phyllodes were conducted using a *CIRAS-1* portable differential CO_2/H_2O infrared gas analyser (*PP Systems*, Hitchin, UK), which has a temperature controlled leaf chamber. A phyllode area of 2.5 cm^2 was enclosed in the leaf chamber at temperature gradients from 20 to 40 °C, 75 % relative humidity, PPFD 0-1 200 $\mu mol\ m^{-2}\ s^{-1}$, an ambient CO_2 concentration, and an air-flow rate of 3.33 $cm^3\ s^{-1}$. For studying PS2, each detached phyllode was put in a 50 cm^3 clear plastic test tube filled with distilled water. This test tube was then submerged in a temperature-controlled water bath (model *9505*, *Polyscience*, USA) whose temperature was adjusted to

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Abbreviations: Chl – chlorophyll; E – transpiration rate; F_m – maximum fluorescence yield; F_v – variable fluorescence; $\Delta F/F'_m$ – effective PS2 efficiency under irradiance-adapted conditions; NPQ – non-photochemical quenching *via* xanthophyll cycle; PPFD – photosynthetic photon flux density; P_N – photon-saturated rate of photosynthetic CO_2 fixation; PS2 – photosystem 2; q_P – photochemical quenching; q_N – non-photochemical quenching; g_s – stomatal conductance; R_D – dark respiration rate.

20, 25, 30, 35, and 40 °C, respectively, for 45 min. Determinations of Chl fluorescence parameters were conducted according to Yu and Ong (2000). All experiments were repeated three times with a total of six plants. Multiple analysis of variance was done using Tukey test ($p \leq 0.05, n = 6$).

P_N increased from 10.22 μmol(CO_2) m^{-2} s^{-1} at 20 °C to 22.00 μmol(CO_2) m^{-2} s^{-1} at 30 °C, and then decreased to 18.20 μmol(CO_2) m^{-2} s^{-1} when the temperature was increased to 37 °C (Fig. 1*A*). The quantum yield of photosynthesis increased from 0.0472 mol(CO_2) mol^{-1}(quantum) at 20 °C to 0.0656 mol(CO_2) mol^{-1}(quantum) at 30 °C, which remained constant as the temperature was in-creased further to 37 °C (Fig. 1*B*). The rate of dark respiration (R_D) increased from 1.04 μmol(CO_2) m^{-2} s^{-1} at 20 °C to 3.05 μmol(CO_2) m^{-2} s^{-1} at 37 °C (Fig. 1*C*). The transpiration rate (*E*) increased from 1.50 mmol(H_2O) m^{-2} s^{-1} at 20 °C to 2.92 mmol(H_2O) m^{-2} s^{-1} at 25 °C, and a great increase to 9.90 mmol(H_2O) m^{-2} s^{-1} at 37 °C followed (Fig. 1*D*). The stomatal conductance (g_s) increased from 158.31 mmol(H_2O) m^{-2} s^{-1} at 20 °C to 565.29 mmol (H_2O) m^{-2} s^{-1} at 32 °C; it then decreased to 330.35 mmol (H_2O) m^{-2} s^{-1} when the temperature was increased to 37 °C (Fig. 1*E*).

No significant changes in photochemical efficiency of PS2 (F_v/F_m, see Genty *et al.* 1989, Van Kooten and Snel 1990) in the temperature range of 20-40 °C were observed (Fig. 1*F*). Quantum yield of non-cyclic electron transport ($\Delta F/F'_m$, see Genty *et al.* 1989, Van Kooten and Snel 1990) generally declined as temperature increased (Fig. 1*G*). The value of non-photochemical quenching (NPQ, see Havaux *et al.* 1991) *via* the xanthophyll cycle increased significantly with increasing temperature from 20 to 40 °C (Fig. 1*H*). Photochemical quenching (q_P, see Havaux *et al.* 1991) of the phyllodes remained stable between 20 and 30 °C, but declined slightly between 30 and 40 °C (Fig. 1*I*). Similar to NPQ, non-photochemical quenching (q_N, see Havaux *et al.* 1991) increased with increasing temperature from 20 to 40 °C, but the magnitude of increase was smaller than that of NPQ.

Our results showed that P_N of *A. mangium* phyllodes had an optimum temperature range of 30-32 °C. R_D, g_s,

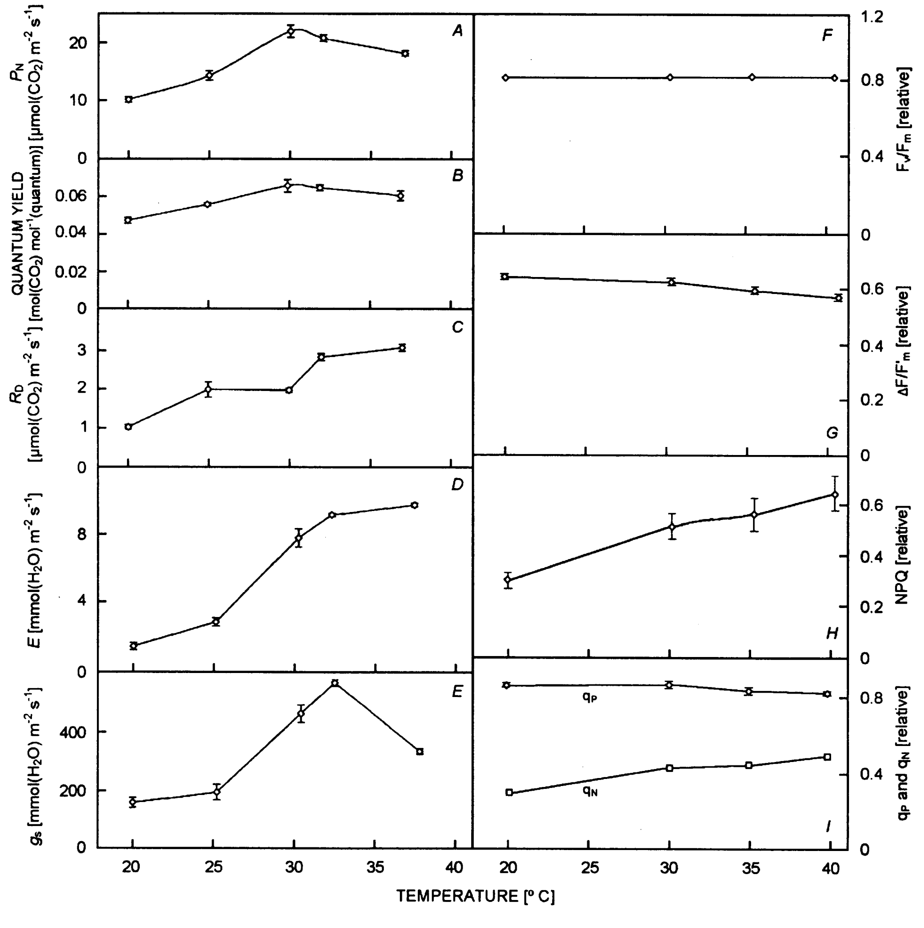

Fig. 1. The changes in photon-saturated net photosynthetic rate, P_N (*A*), quantum yield of photosynthesis (*B*), dark respiration rate, R_D (*C*), transpiration rate, *E* (*D*), stomatal conductance, g_s (*E*), photochemical efficiency of photosystem 2, F_v/F_m (*F*), quantum yield of non-cyclic electron transport, $\Delta F/F'_m$ (*G*), non-photochemical quenching *via* xanthophylls cycle, NPQ (*H*), and photochemical quenching (q_P) and non-photochemical quenching (q_N) (*I*) of *A. mangium* phyllodes in response to temperature increase. Means ± S.E.

and *E* of *A. mangium* phyllodes were also low at 20 °C. However, F_v/F_m and $\Delta F/F'_m$ at 20 °C were similar, or slightly higher, than those observed at the optimum temperature (32 °C). Thus the 50 % reduction in P_N at 20 °C was not the result of the down-regulation of photochemical efficiency of PS2. Such reductions might partially be caused by the reduction in g_s, as g_s at 20 °C was only 28 % of the maximum value observed at 32 °C. However, the inhibition of P_N in the *A. mangium* phyllodes at the lower temperature (20 °C) could not be fully accounted for by stomatal limitations. As in the low temperature-exposed (5-20 °C) whole plants of *Lycopersicon esculentum* (Martin and Ort 1985), *Olea europaea* (Bongi and Long 1987), *Triticum aestivum* (Hurry and Huner 1991), and *Zea mays* (Nie *et al.* 1992), the decreased g_s played only a minor role in the temperature limitation of photosynthesis. Short-term exposures of whole plants to low temperature usually result in significant reductions of P_N (Hurry *et al.* 1998). This is principally due to the accumulation of soluble saccharides, which suppresses photosynthesis by reducing orthophosphate cycling from the cytosol back to the chloroplasts, thus limiting the synthesis of ATP needed in the regeneration of ribulose-1,5-bisphosphate (Hurry *et al.* 1998). Long-term exposure of *Pinus sylvestris*, an evergreen woody perennial, to low growth temperatures also resulted in a depression of P_N (Öquist and Martin 1986). This was associated with lower photon-saturated rates of non-cyclic photosynthetic electron transport and reductions in the size of the functional plastoquinone pool (Öquist and Martin 1986).

P_N was photon-saturated at phyllode temperatures of 30-32 °C, similarly as observed in some tropical mangrove species (Ball *et al.* 1988). The maximum P_N of *A. mangium* phyllodes was 22.00±1.06 µmol(CO_2) m^{-2} s^{-1}, a relatively high value compared to other tropical tree species. For example, P_N ranged from 13 to 16 µmol(CO_2) m^{-2} s^{-1} in some secondary tropical trees (Koyama 1981). Hall (2001) also pointed out that, in general, plant species with higher optimal temperature for photosynthesis showed higher P_N. Moreover, in the temperature range of 27-37 °C, P_N of *A. mangium* phyllodes was $\geq$ 82 % of the maximum P_N observed at 30-32 °C. This temperature range was identical to the daily temperature variation of the experimental site, where the *A. mangium* plants were grown. As the climate in Singapore is not seasonal, our results reflected the degree to which the *A. mangium* plants must adjust its photosynthetic processes to daily temperature variations throughout the day.

The highest quantum yield of photosynthesis of *A. mangium* phyllodes was observed at 30 °C, the same as that for P_N. This result indicated that the photosynthetic photon utilisation efficiency was high at this high temperature. Moreover, the quantum yield of photosynthesis and P_N of *A. mangium* phyllodes exhibited only a small decrease (8-17 %) when the phyllode temperature was increased to 37 °C, indicating that *A. mangium* was well-adapted to the high temperature of tropical climate, in terms of photosynthetic carbon gain and photon use efficiency. However, this adaptation occurred at the cost of higher respiratory losses. This was evident from the observation that R_D of phyllodes increased by 56 % at 37 °C, compared with that at 30 °C. The increased R_D at high temperatures could be interpreted as an increase in mitochondrial consumption of reducing equivalents generated by the chloroplast electron transport chain, and as an indication of increased metabolic activity with increasing phyllode temperature (Hurry *et al.* 1996). Re-establishment of the balance between photosynthesis and carbon metabolism is a key element in high temperature and high irradiance acclimation response of plants (Hurry *et al.* 1996). The ability of *A. mangium* phyllodes to up-regulate respiratory metabolism at high temperatures might play an important role not only in preventing photoinhibition of PS2 and avoiding oxidative injury associated with high temperatures, but also in increasing cytosolic CO_2 by 56 % and thereby increasing the non-cyclic photosynthetic electron transport rate. For example, the mitochondrial electron transport was important in preventing photoinhibition in *Pisum sativum* protoplasts (Saradadevi and Raghavendra 1992).

At 37 °C, *A. mangium* phyllodes exhibited a 17 % decrease in P_N as compared with that of the maximal P_N at 30 °C. This decrease in P_N was partially due to the inhibition of PS2 activity as well as the decline in g_s. $\Delta F/F'_m$ showed an 8 % decrease. At the same time, g_s of phyllodes decreased by 42 % at 37 °C, compared with that at 32 °C. High temperature induced decreases in g_s were also observed in two other tropical tree species, *Maranthes corymbosa* and *Eucalyptus tetrodonta* (Berryman *et al.* 1994). The quantum yield of phyllodes of *A. mangium* decreased by 8 % at 37 °C, as compared to the maximal value at 30 °C. This was, probably, caused by the decreased photochemical quenching and increased photorespiration at high temperatures.

Temperature induced changes in Chl fluorescence parameters were recorded in many crop plants, such as *Zea mays* (Öquist and Wass 1988) and *Phaseolus vulgaris* (Pastenes and Horton 1999), and tree species (Roden and Ball 1996, Dreyer *et al.* 2001, Ishida *et al.* 2001). Although the photochemical events of photon absorption, energy transfer, and charge separation associated with PS2 and PS1 are insensitive to temperature in the biologically relevant temperature range of 0 to 50 °C (Mathis and Rutherford 1987), the response of photochemical efficiency of PS2 to temperature change is species specific. In the present study, F_v/F_m of *A. mangium* phyllodes was maintained at 0.81-0.82 within the phyllode temperature range of 20-40 °C, indicating that the PS2 exhibited high tolerance to high temperatures. Such high PS2 efficiency allowed the plants to grow well in Singapore, in a temperature range of 26-33 °C (Hew and Yong 1994). In addition, the high F_v/F_m value in phyllodes of *A. mangium* suggested no photoinhibition. In an-other study, whole plants of *Alocasia macrorrhiza*, exposed to 42-46 °C for 3 h at a PPFD of 1 650 μmol m^{-2} s^{-1}, did not exhibit any change in F_v/F_m (Königer *et al.* 1998). In contrast, F_v/F_m of seedlings of seven temperate tree species (*Acer pseudoplatanus*, *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsio*, *Juglans regia*, *Quercus petraea*, and *Quercus robur*) decreased when the plants were treated at a temperature close to 38 °C (Dreyer *et al.* 2001). A rapid photo-inactivation of PS2 was observed at high temperature (40 °C) in *Spinacia oleracea* (Yamane *et al.* 1998). A lower F_v/F_m with increasing leaf temperature up to 38 °C was observed in *Cucumis sativus* (Taub *et al.* 2000).

The high tolerance of *A. mangium* phyllodes to high temperature was closely related to its effective thermal dissipation of excess absorbed photon energy, *i.e.* non-photochemical quenching *via* the xanthophyll cycle (NPQ). NPQ is a measure of thermal dissipation of excess absorbed photons (Bilger and Björkman 1990). We found that NPQ of *A. mangium* phyllodes increased steadily with increasing phyllode temperature, indicating NPQ played a crucial role in protecting the PS2 of the phyllodes from the damages associated with high temperature and high PPFD in the tropics. As the high NPQ capacity is usually correlated with higher xanthophyll cycle activity (Bilger and Björkman 1990, Demmig-Adams and Adams 1992), the high NPQ observed in *A. mangium* in response to high temperature was probably associated with the big pool size of xanthophyll cycle pigments in the phyllodes. The high NPQ in the phyllodes of *A. mangium* suggested the genetic potential of *A. mangium* to allow reasonable photosynthetic performance at high temperatures above the optimal. In addition, NPQ is not only associated with xanthophyll cycle activity (Lee *et al.* 2001), as Horton (1999) pointed out that NPQ can also be brought about by excitation quenching associated with the establishment of a pH gradient across the thylakoid membranes, amplified by a high de-epoxidation state. High temperatures occur when high PPFD is incident on the phyllode surfaces. The previous study showed that the phyllode temperature could reach 36.5 °C in April or August, when air temperature could increase to 36 °C (Yu 2002). The increased NPQ contributed to the maintenance of a high rate of photosynthetic CO_2 uptake and to a reduction in the risk of photoinhibition at the high temperatures of tropical climate.

References

Atkins, O.K., Schortemeyer, M., McFarlane, N., Evans, J.R.: Variation in the components of relative growth rate in ten *Acacia* species from contrasting environments. – Plant Cell Environ. **21**: 1007-1017, 1998.

Ball, M.C., Cowan, I.R., Farquhar, G.D.: Maintenance of leaf temperature and the optimisation of carbon gain in relation to water loss in a tropical mangrove forest. – Aust. J. Plant Physiol. **15**: 263-276, 1988.

Berryman, C.A., Eamus, D., Duff, G.A.: Stomatal responses to a range of variables in two tropical tree species grown with CO_2 enrichment. – J. exp. Bot. **45**: 539-546, 1994.

Bilger, W., Björkman, O.: Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*. – Photosynth. Res. **25**: 173-185, 1990.

Bongi, G., Long, S.P.: Light dependent damage to photosynthesis in olive leaves during chilling and high temperature stress. – Plant Cell Environ. **10**: 241-249, 1987.

Demmig-Adams, B., Adams, W.W., III: Photoprotection and other responses of plants to high light stress. – Annu. Rev. Plant Physiol. Plant mol. Biol. **43**: 599-626, 1992.

Dreyer, E., Le Roux, X., Montpied, P., Daudet, F.A., Masson, F.: Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. – Tree Physiol. **21**: 223-232, 2001.

Genty, B., Briantais, J.-M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. biophys. Acta **990**: 87-92, 1989.

Hall, A.E.: Crop Responses to Environment. – CRC Press, Boca Raton – London – New York – Washington 2001.

Havaux, M., Strasser, R.J., Greppin, H.: A theoretical and experimental analysis of the q_P and q_N coefficients of chloro-phyll fluorescence quenching and their relation to photo-chemical and non-photochemical events. – Photosynth. Res. **27**: 41-55, 1991.

Hew, C.S., Yong, J.W.H.: Growth and photosynthesis of *Oncidium 'Goldiana'*. – J. hort. Sci. **69**: 809-819, 1994.

Horton, P.: Are grana necessary for regulation of light harvesting? – Aust. J. Plant Physiol. **26**: 659-669, 1999.

Hurry, V., Huner, N., Selstam, E., Gardeström, P., Öquist, G.: Photosynthesis at low growth temperatures. – In: Raghavendra, A.S. (ed.): Photosynthesis. A Comprehensive Treatise. Pp. 238-249. Cambridge University Press, Cambridge 1998.

Hurry, V.M., Huner, N.P.A.: Low growth temperature effects a differential inhibition of photosynthesis in spring and winter-wheat. – Plant Physiol. **96**: 491-497, 1991.

Hurry, V.M., Keerberg, O., Pärnik, T., Öquist, G., Gardeström, P.: Effect of cold hardening on the components of respiratory decarboxylation in the light and in the dark in leaves of winter rye. – Plant Physiol. **111**: 713-719, 1996.

Ishida, A., Nakano, T., Matsumoto, Y., Sakoda, M., Ang, L.H.: Diurnal changes in leaf gas exchange and chlorophyll fluorescence in tropical tree species with contrasting light requirements. – Ecol. Res. **14**: 77-88, 1999.

Ishida, A., Nakano, T., Sekikawa, S., Maruta, E., Masuzawa, T.: Diurnal changes in needle gas exchange in alpine *Pinus pumila* during snow-melting and summer seasons. – Ecol. Res. **16**: 107-116, 2001.

Königer, M., Harris, G.C., Pearcy, R.W.: Interaction between photon flux density and elevated temperatures on photoinhibition in *Alocasia macrorrhiza*. – Planta **205**: 214-222, 1998.

Koyama, H.: Photosynthetic rates in lowland rainforest trees of peninsular Malaysia. – Jap. J. Ecol. **31**: 361-369, 1981.

Lee, H.Y., Hong, Y.N., Chow, W.S.: Photoinactivation of photosystem II complexes and photoprotection by non-functional neighbours in *Capsicum annuum* L. leaves. – Planta **212**: 332-342, 2001.

Martin, B., Ort, D.R.: The recovery of photosynthesis in tomato subsequent to chilling exposure. – Photosynth. Res. **6**: 121-132, 1985.

Mathis, P., Rutherford, A.W.: The primary reactions of photosystems I and II of algae and higher plants. – In: Amesz, J. (ed.): Photosynthesis. Pp. 63-96. Elsevier Science Publishers, Amsterdam 1987.

Mok, C.K., Cheah, L.C., Chan, Y.K.: Site management and productivity of *Acacia mangium* in humid tropical Sumatra, Indonesia. – In: Nambiar, E.K.S., Tiarks, A., Cossalter, C., Ranger, J. (ed.): Site Management and Productivity in Tropical Plantation Forests. Pp. 87-94. Center for International Forestry Research, Bogor 2000.

Nie, G.Y., Long, S.P., Baker, N.R.: The effects of development at sub-optimal growth temperatures on photosynthetic capacity and susceptibility to chilling-dependent photoinhibition in *Zea mays*. – Physiol. Plant. **85**: 554-560, 1992.

Öquist, G., Martin, B.: Cold climates. – In: Baker, N.R., Long, S.P. (ed.): Photosynthesis in Contrasting Environments. Pp. 237-293. Elsevier Science Publishers, Amsterdam 1986.

Öquist, G., Wass, R.: A portable, microprocessor operated instrument for measuring chlorophyll fluorescence kinetics in stress physiology. – Physiol. Plant. **73**: 211-217, 1988.

Pastenes, C., Horton, P.: Resistance of photosynthesis to high temperature in two bean varieties (*Phaseolus vulgaris* L.). – Photosynth. Res. **62**: 197-203, 1999.

Roden, J.S., Ball, M.C.: Growth and photosynthesis of two eucalypt species during high temperature stress under ambient and elevated [CO_2]. – Global Change Biol. **2**: 115-128, 1996.

Saradadevi, K., Raghavendra, A.S.: Dark respiration protects photosynthesis against photoinhibition in mesophyll protoplasts of pea (*Pisum sativum*). – Plant Physiol. **99**: 1232-1237, 1992.

Sim, B.L.: Research on *Acacia mangium* in Sabah: A review. – In: Turnbull, J.W. (ed.): Australian *Acacias* in Developing Countries. Pp. 164-166. Australian Center for International Agricultural Research, Canberra 1986.

Taub, D.R., Seemann, J.R., Coleman, J.S.: Growth in elevated CO_2 protects photosynthesis against high-temperature damage. – Plant Cell Environ. **23**: 649-656, 2000.

Van Kooten, O., Snel, J.F.H.: The use of chlorophyll fluorescence nomenclature in plant stress physiology. – Photosynth. Res. **26**: 147-150, 1990.

Yamane, Y., Kashino, Y., Koike, H., Satoh, K.: Effects of high temperatures on the photosynthetic systems in spinach: Oxygen-evolving activities, fluorescence characteristics and denaturation process. – Photosynth. Res. **57**: 51-59, 1998.

Yu, H.: Fast Growth of *Acacia mangium*, a Result of Efficient Light Utilization and Carbon Assimilation? – Ph.D. Dissertation. National University of Singapore 2002.

Yu, H., Ong, B.L.: Photosynthesis and antioxidant enzymes of phyllodes of *Acacia mangium*. – Plant Sci. **159**: 107-115, 2000.

Yu, H., Ong, B.-L.: Responses of *Acacia mangium* seedlings to different irradiances. – Photosynthetica **39**: 477-479, 2001.

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