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Scientia Horticulturae 109 (2006) 101–105

SCIENTIA HORTICULTURAE

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Short communication

Photosynthetic irradiance-response in leaves of dwarf coconut palm (*Cocos nucifera* L. '*nana*', Arecaceae): Comparison of three models

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Received 23 March 2005; received in revised form 21 September 2005; accepted 28 February 2006

Abstract

Experimental data of irradiance-response curves of photosynthesis, obtained from independent experiments with the Brazilian Green Dwarf coconut palm genotype, were used to fit three empirical models with the aim to compare their adequacies. The non-rectangular and rectangular hyperbolas and the exponential models were compared. The rectangular hyperbola and the exponential models were quantitatively adequate to describe the irradiance-response of photosynthesis in dwarf coconut in all the situations studied. The photosynthetic parameters showed good correlation with the measured values when estimated by the rectangular hyperbola and exponential but the later estimated a more realistic light-saturated rate and the apparent quantum yield of photosynthesis. The NRH was less adequate for estimate the light-saturated photosynthesis and dark respiration universally, but could be used for research purposes since it contains an important qualitative parameter, the convexity term relating physical to total resistances to CO_2 diffusion into the chloroplasts. The results allow suggesting the exponential model as a rapid, simple, quantitatively and qualitatively adequate option for accessing information from the photosynthetic irradiance-response in dwarf coconut palm.

Keywords: Apparent quantum yield; Compensation irradiance; Convexity term; Dark respiration; Light-saturated rate of net photosynthesis

1. Introduction

Complex mechanistic models of photosynthesis such the biochemical model of Farquhar et al. (1980) for C_3 leaves, has been adopted in studies of ecological and physiological modeling, since it is capable of describing underlying processes that might not be well described by empirical models. However, it requires rather extensive calibration of a number of parameter as well as complex parameterization procedures (Cannell and Thomley, 1998). Moreover, detailed treatment of biochemical processes in biochemical photosynthesis models not always is advantageous over the simpler leaf photosynthesis models (Gao et al., 2004). Nevertheless, the empirical models have been used extensively in ecophysiology for accessing and exploring information derived from irradiance-response curves of photosynthesis as, for example, in studies of the effects of biotic (Habermann et al., 2003) and abiotic stresses such as drought (Escalona et al., 1999), salinity (Krauss and Allen, 2003), soil flooding (Mielke et al., 2003) and temperature (Peri et al., 2005), since they have simple formulas, can be easily parameterized and their parameters have a straightforward interpretation.

The objective of the present study was to compare the three traditional models (rectangular and non-rectangular hyperbolas and exponential) for describing the photosynthetic irradiance-response curve using data from dwarf coconut palm. We tested the hypothesis that the three models are quantitatively adequate but behave distinctly when used for estimating the main photosynthetic parameters.

2. Material and methods

2.1. Sites and plant material

The analyses were performed using the photosynthetic irradiance-response curves measured in adult and young plants of Brazilian Green Dwarf coconut (*Cocos nucifera* L. '*nana*') genotype grown under field and greenhouse conditions,

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doi:10.1016/j.scienta.2006.02.030

respectively. The sites (1–4) of data collection in the field were described in Gomes et al. (2002). The greenhouse experiment (site 5) was conducted at the Plant Growth Center of the Federal University of Viçosa, Brazil (20°45′S, 42°52′W, 648 m asl), where potted seedlings of the BGD coconut genotype were grown for 7 months. At the moment of measurements the plants had 1.2 m and 5–7 expanded leaves. Intact leaves of rank 2 and 9 (counted from the top down) were used for the gas exchange measurements in young and adult palms, respectively. A total of 32 irradiance-response curves were used in the analysis: 3 from site 1, 9 from site 2, 11 from site 3, 3 from site 4 and 6 from site 5.

2.2. Photosynthetic measurements

The measurements were performed always from 7:30 to 11:00 h using a Portable Photosynthesis System LI-6400 (Li-Cor, USA) equipped with an artificial irradiance source 6400-02B RedBlue. It used the "light curve" routine of the software OPEN 3.4, in seven levels of photosynthetic photon flux density (PPFD, 50, 100, 200, 400, 800, 1200 and 1600 μmol photons $m^{-2}\ s^{-1}$) in a decreasing order. The minimum time allowed for the reading stabilization at each level of PPFD was 120 s, and the maximum time for saving each reading was 150 s. It was set a flow rate of 400 μmol s^{-1} and a maximum coefficient of variation (C.V.) of 1%. The values of atmospheric CO_2 concentration and of leaf-to-air water vapour pressure deficit inside the assimilation chamber were 376 ± 11 μmol mol^{-1}, 1.4 ± 0.5 kPa, respectively. Mean leaf temperature was 28.6 ± 2.2 °C, depending on the site and increased 0.8 °C on average with increasing irradiance. Due to the partial shading caused by the uppermost leaves, the leaves used for the gas exchange measurements were not exposed to direct radiation before the measurements. However, no stomatal limitation was observed at the start point of each curve (maximum PPFD), as indicated by the relation between intercellular to atmospheric CO_2 concentration (C_i/C_a) (data not shown).

2.3. Description of the models

Three empirical models were tested:

Non-rectangular hyperbola, NRH (Marshall and Biscoe, 1980)

$$A_n = \left\{ \frac{[A_{max} + (\alpha PPFD) - [(A_{max} + (\alpha PPFD))^2 - (4\alpha\theta PPFD A_{max})]^{0.5}}{(2\theta)} \right\} - R_d$$

Rectangular hyperbola, RH (Thomley, 1976)

$$A_n = \left\{ \frac{(A_{max}\alpha PPFD)}{[A_{max} + (\alpha PPFD)]} \right\} - R_d$$

Exponential, EXP (Iqbal et al., 1997)

$$A_n = \left\{ A_{max} \left[1 - \exp\left(\frac{-\alpha PPFD}{A_{max}} \right) \right] \right\} - R_d$$

where A_n is the rate of net photosynthesis (μmol $CO_2\ m^{-2}\ s^{-1}$); A_{max} the irradiance-saturated rate of gross photosynthesis (μmol $CO_2\ m^{-2}\ s^{-1}$) ($A_{max} = A_{nmax} + R_d$, where A_{nmax} is the irradiance-saturated A_n and R_d is the dark respiration rate (μmol $CO_2\ m^{-2}\ s^{-1}$), corresponding to the value of A_n when PPFD = 0 μmol photons $m^{-2}\ s^{-1}$); α is apparent quantum yield of photosynthesis; θ is a dimensionless convexity term. For correlation analysis between measured and estimated values, "measured" α was estimated by the linear regression of A_n to PPFD < 200 μmol $m^{-2}\ s^{-1}$ (Escalona et al., 1999). In the linear equation, α is the coefficient of the independent term (slope of the curve). Measured A_{nmax} is the mean value of A_n when PPFD > 800 μmol photons $m^{-2}\ s^{-1}$.

2.4. Statistical analysis

Every model was fitted to measured data from each one of the 32 irradiance-response curves using the Levemberg–Marquardt algoritim of the non-linear least squares estimate routine of the software Statistica 6.0 (StatSoft Inc.). The initial values for A_{max}, α, R_d and θ were set at 5 μmol $CO_2\ m^{-2}\ s^{-1}$, 0.01 mol $CO_2\ mol^{-1}$ photons, 0.1 μmol $CO_2\ m^{-2}\ s^{-1}$ and 0.1, respectively, according to the coherence of the predicted values. The adequacy (goodness-of-fit) of the models was verified by plotting the modeled curve for all data with the mean measured values for each site, by the analysis of residuals, i.e., the deviations between the measured and predicted values, and by a special F-test (Pachepsky et al., 1996). Correlation analyses between predicted and measured (or linearly estimated) values were also performed and the r^2 was used as an accessory indicator for the validation of the models.

3. Results

All three models showed a good fit ($r^2 > 0.90$) to the experimental data with good correspondence with the shapes of the mean measured values at all sites (Fig. 1). Goodness-of-fit was confirmed for all sites by the F-test (Table 1) indicating that the three models were adequate. On the other hand, the absolute value of F for the NRH and RH were larger than that for EXP.

The RH and EXP models showed a random distribution of the residuals around the predicted values at all sites (Fig. 2). Under high irradiance, the NRH showed a clear underestimation of A_n at the site 1 and overestimation at the sites 2 and 5 (Fig. 2).

A linear trend was observed between measured and predicted values of A_{nmax} by the RH ($r^2 = 0.80$–0.95, Fig. 3B) but the values predicted by the NRH showed a large scatter with poor linear correlation at sites 2, 3 and 5 (Fig. 3A). The two hyperbolas estimated higher values of A_{nmax} as compared to measured light-saturated A. While predicted and measured R_d showed good correlations at all sites when estimated by the RH (Fig. 3E, $r^2 = 0.89$) and EXP (Fig. 3F, $r^2 = 0.83$), this parameter was lower than the measured R_d at site 2 and higher at site 4 when estimated by the NRH (Fig. 3D). Comparing α estimated by the non-linear models (predicted)

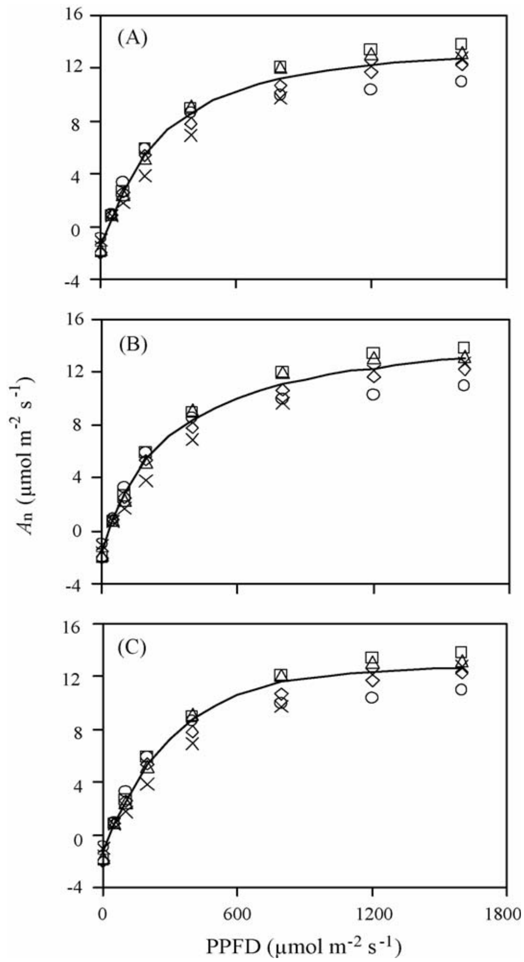

Fig. 1. Irradiance-response curves of net photosynthesis (A_n) in dwarf coconut. The points are the measured mean values of A_n at sites 1 (◇), 2 (△), 3 (□), 4 (×) and 5 (○) and the lines represent the non-rectangular hyperbola (A), the rectangular hyperbola (B) and the exponential (C) models.

with that estimated by linear regression (quoted as measured), it was observed that all three models showed good linear correlation with mean r^2 varying from 0.69 to 0.71 (Fig. 3G, H), but, like A_{nmax}, α was higher than the values estimated by linear regression when predicted by the two hyperbolas. The three parameters were better estimated by the exponential model, whose outputs were linearly correlated with measured values (Fig. 3C, F, I).

4. Discussion

The special F-test (Pachepsky et al., 1996) allowed comparison of the variability of predictions (lack-of-fit mean square) with the variability of data (pure error mean square). It must be noted that the denominator of F (data variability) is the same for all three models so the numerator characterizes the lack-of-fit of the model. The lower absolute value of F for EXP may indicate a better quantitative performance of this model when compared to the hyperbolas. On the other hand, whereas the NRH model was considered quantitatively adequate by the F-test (Table 1), it was shown to be inadequate for two of five sites by the residual analysis (Fig. 2).

Table 1
F-test ($p < 0.05$) for accessing the quantitative performances of the non-rectangular (NRH) and rectangular (RH) hyperbolas and the exponential (EXP) models describing the irradiance-response of photosynthesis in dwarf coconut

Model	Site	F	F (Tab)
NRH	1	1.89	3.06
	2	0.48	2.56
	3	0.30	2.49
	4	0.11	3.05
	5	1.56	2.61
	All	1.42	4.12
RH	1	2.05	2.90
	2	1.92	2.37
	3	0.20	2.33
	4	0.07	2.90
	5	3.53^{NS}	2.45
	All	1.47	3.27
EXP	1	1.93	2.90
	2	0.36	2.37
	3	0.80	2.33
	4	0.16	2.90
	5	1.29	2.45
	All	1.17	3.27

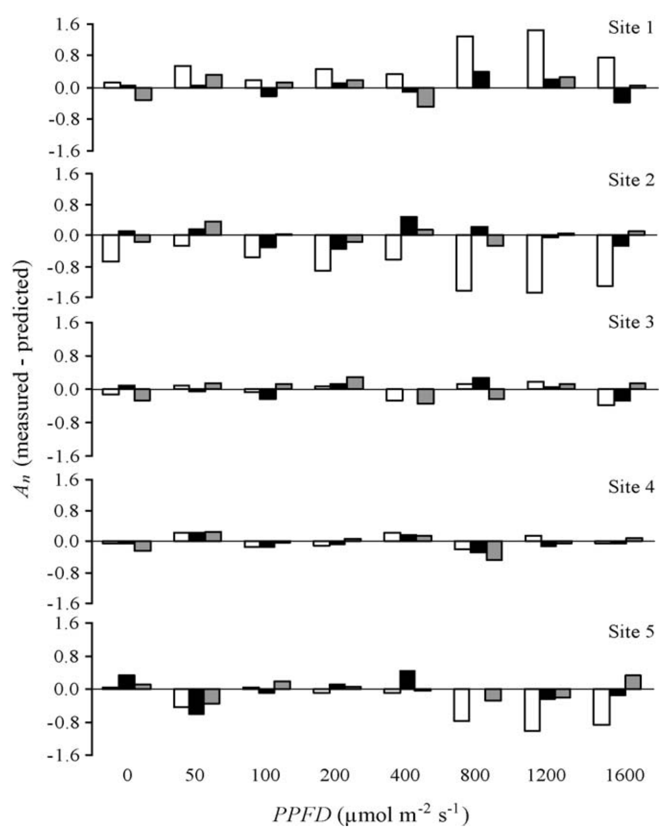

Fig. 2. Measured minus predicted values of net photosynthesis (A_n) obtained after adjusting the non-rectangular hyperbola (white), the rectangular hyperbola (black) and the exponential (gray) models to the field data of irradiance-response curves of photosynthesis in dwarf coconut at the five sites.

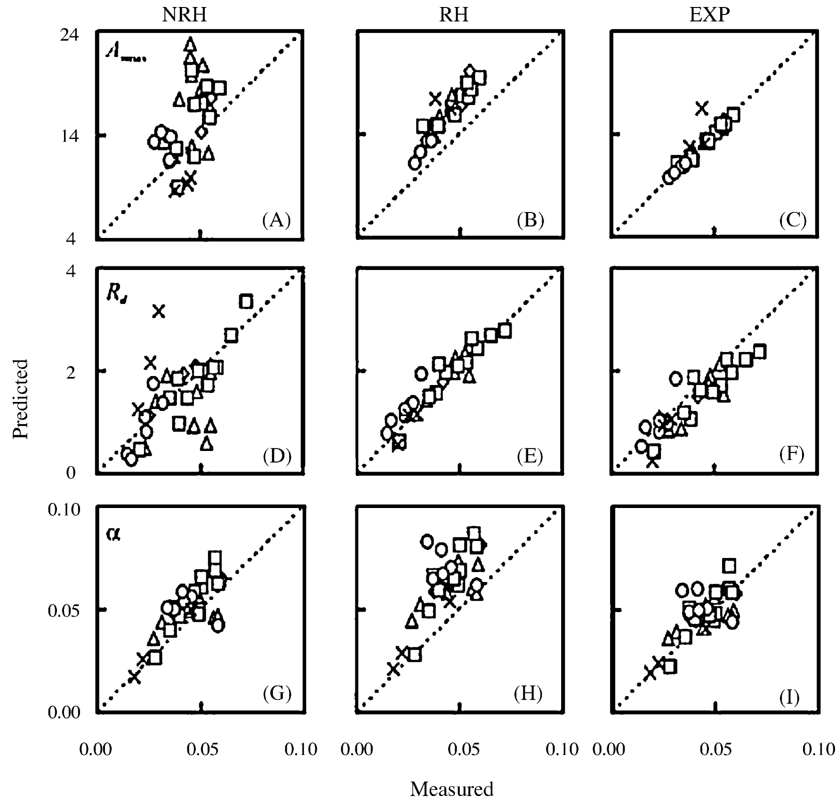

Fig. 3. Predicted and measured values of the irradiance-saturated net photosynthesis (A_{nmax}, A–C), dark respiration (R_d D–F) and apparent quantum yield (α, G–I) in dwarf coconut. NRH, non-rectangular hyperbola; RH, rectangular hyperbola; EXP, exponential. Sites 1 (◇), 2 (△), 3 (□), 4 (×) and 5 (○). The 1:1 lines (dotted) are shown.

The RH gave higher A_{nmax} and α, when compared to measured (or linearly estimated) values, as has been observed in other studies (Lamade and Setiyo, 1996; Mielke et al., 2003). Nevertheless, this model was quantitatively adequate for dwarf coconut and could be used as a submodel for predictive calculations in productivity models. Dufrene et al. (1990) used a RH as component of a complex model to estimate canopy assimilation, which allowed understanding the links between productivity and climatic factors in oil palm. Moreover, high predicted α as compared to the linearly estimated values (Fig. 3) could be due, in part, to the use of a linearly underestimated α for comparison. Using linear regression to estimate α of modeled light curves with $\theta = 0.89$, Leverenz et al. (1990) observed an underestimation of α by about 9%.

The EXP model was also quantitatively adequate to describe the photosynthetic irradiance-response in dwarf coconut and provided a more accurate and realistic estimation of the photosynthetic parameters when compared to the two hyperbolic models. Like the RH it has few and easily interpreted parameters and could be used for predictive purposes either isolated or as part of non-linear mixed models (Peek et al., 2002).

It was demonstrated here that NRH was less adequate for A_{nmax} and R_d predictions universally, which suggest its limited applicability for predictive purposes. Nevertheless, this model has been preferred for research purposes either alone or as a part of a larger model to study the mechanisms of photosynthesis (Peri et al., 2005). A mean value of 0.50 for its convexity term (θ), as estimated in the present work (data not shown), was interpreted to be a result of a low physical limitation (high stomatal conductance) as compared to internal (mesophyll and biochemical) resistances to CO_2 diffusion into the chloroplast (Marshall and Biscoe, 1980). Although more specific experiments are necessary to strengthen that interpretation, high values of stomatal conductance (0.3–0.7 mol H_2O m^{-2} s^{-1}) usually measured in dwarf coconut varieties (Passos et al., 1999; Gomes et al., 2002) corroborate the present results. On the other hand, the value of 0.50, in spite of being considered low when compared to other C_3 species (Ögren, 1993), could be due to the adaptation of coconut to high light environments. According to Leverenz (1994), as the mismatch between the gradients of A_{max} and of PPFD through the leaf increases, the value of θ decreases more from its intrinsic value in the chloroplasts so that high irradiance-adapted plants may show very low θ, depending upon the species. Thomas and Bazzaz (1999) estimated values of θ ranging from 0.20 to 0.80 for tree species of dipterocarp forest of the Indo-Malayan region.

The results allow concluding that the rectangular hyperbola and the exponential models were quantitatively adequate for fitting experimental data of irradiance-response curves in dwarf coconut palm at all studied sites but A_{nmax} and α were more realistic when estimated by the exponential. The NRH was less adequate for estimate A_{nmax} and R_d universally, but could be used for research purposes since it contains an important qualitative parameter, the convexity term. The use of exponential models for accessing the information of the photosynthetic irradiance-response curves of Brazilian Green Dwarf coconut is recommended.

Acknowledgements

We thank Dr. Francisco Lobo and anonymous referees for helpful comments and discussion. This work was supported by the Universidade Estadual de Santa Cruz (UESC), and by the Brazilian Government, through its financial agencies, CAPES and CNPq.

References

Cannell, M.G.R., Thomley, J.H.M., 1998. Temperature and CO_2 responses of leaf and canopy photosynthesis: a clarification using the non-rectangular hyperbola model of photosynthesis. Ann. Bot. 82, 883–892.

Dufrene, E., Ochs, R., Saugier, B., 1990. Photosynthèse et productivité du palmier à huile em liaison avec les facteurs climatiques. Oleagineux 45, 345–355.

Escalona, J.M., Flexas, J., Medrano, H., 1999. Stomatal and non-stomatal limitations of photosynthesis under water stress in field-grown grapevines. Aust. J. Plant Physiol. 26, 421–433.

Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of the photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149, 78–90.

Gao, Q., Zhang, X., Huang, Y., Xu, H., 2004. A comparative analysis of four models of photosynthesis for 11 plant species in the Loess Plateau. Agric. For. Meteorol. 126, 203–222.

Gomes, F.P., Mielke, M.S., Almeida, A.-A.F., 2002. Leaf gas exchange of green dwarf coconut (*Cocos nucifera* L. var. *nana*) in two contrasting environments of the Brazilian north-east region. J. Hortic. Sci. Biotechnol. 77, 766–772.

Habermann, G., Machado, E.C., Rodrigues, J.D., Medina, C.L., 2003. CO_2 assimilation, photosynthetic light response curves, and water relations of 'Pera' sweet orange plants infected with *Xylella fastidiosa*. Braz. J. Plant Physiol. 15, 79–87.

Iqbal, R.M., Rao, Aur.-R., Rasul, E., Wahid, A., 1997. Mathematical models and response functions in photosynthesis: an exponential model. In: Pessarakli, M. (Ed.), Handbook of photosynthesis. Marcel Dekker Inc., New York, U.S.A., pp. 803–810.

Krauss, K.W., Allen, J.A., 2003. Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. Aquat. Bot. 77, 311–324.

Lamade, E., Setiyo, E., 1996. Variation in maximum photosynthesis of oil palm in Indonesia: comparison of three morphologically contrasting clones. Plantat. Rech. Develop. 3, 429–438.

Leverenz, J.W., Falk, S., Pilstrom, C.-M., Samuelson, G., 1990. The effects of photoinhibition on the photosynthetic light-response curve of green plant cells (*Chlamidomonas reinhardtii*). Planta 182, 161–168.

Leverenz, J.W., 1994. Factors determining the nature of the irradiance dosage response curve of leaves. In: Baker, N.R., Bowyer, J.R. (Eds.), Photoinhibition of Photosynthesis. From Molecular Mechanisms to the Field. Bios Scientific Publishers, Oxford, pp. 239–254.

Marshall, B., Biscoe, P.V., 1980. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance. J. Exp. Bot. 31, 29–39.

Mielke, M.S., Almeida, A-A.F., Gomes, F.P., Aguilar, M.A.G., Mangabeira, P.A.O., 2003. Leaf gas exchange, chlorophyll fluorescence and growth responses of *Genipa Americana* seedlings to soil flooding. Environ. Exp. Bot. 50, 221–231.

Ogren, E., 1993. Convexity of the photosynthetic irradiance-response curve in relation to intensity and direction of irradiance during growth. Plant Physiol. 101, 1013–1019.

Pachepsky, L.B., Hesketh, J.D., Acock, B., 1996. An adequate model of photosynthesis I. Parameterization, Validation and Comparison of Models. Agric. Syst. 50, 209–225.

Passos, E.E.M., Prado, C.H.B.A., Leal, M.L.S., 1999. Condutância estomática, potencial hídrico foliar e emissão de folhas e inflorescencias em três genótipos de coqueiro anão. Agrotrópica 11, 147–152.

Peek, M.S., Russek-Cohen, E., Wait, D.A., Forseth, I.N., 2002. Physiological response curve analysis using nonlinear mixed models. Oecologia 132, 175–180.

Peri, P.L., Moote, D.J., McNeil, D.L., 2005. Modelling photosynthetic efficiency (α) for the light-response curve of cocksfoot leaves grown under temperate field conditions. Eur. J. Agron. 22, 277–292.

Thomas, S.C., Bazzaz, F.A., 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80, 1607–1622.

Thomley, J.H.M., 1976. Mathematical models in plant physiology, A quantitative approach to problems in plant and crop physiology. Academic Press, London.