

Photosynthetic responses of young cashew plants to varying environmental conditions

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Abstract – The aim of this study was to characterize gas exchange responses of young cashew plants to varying photosynthetic photon flux density (PPFD), temperature, vapor-pressure deficit (VPD), and intercellular CO₂ concentration (C_i), under controlled conditions. Daily courses of gas exchange and chlorophyll a fluorescence parameters were measured under natural conditions. Maximum CO₂ assimilation rates, under optimal controlled conditions, were about 13 mmol m⁻² s⁻¹, with light saturation around 1,000 mmol m⁻² s⁻¹. Leaf temperatures between 25°C and 35°C were optimal for photosynthesis. Stomata showed sensitivity to CO₂, and a closing response with increasing C_i. Increasing VPD had a small effect on CO₂ assimilation rates, with a small decrease above 2.5 kPa. Stomata, however, were strongly affected by VPD, exhibiting gradual closure above 1.5 kPa. The reduced stomatal conductances at high VPD were efficient in restricting water losses by transpiration, demonstrating the species adaptability to dry environments. Under natural irradiance, CO₂ assimilation rates were saturated in early morning, following thereafter the PPFD changes. Transient F_v/F_m decreases were registered around 11h, indicating the occurrence of photoinhibition. Decreases of excitation capture efficiency, decreases of effective quantum yield of photosystem II, and increases in non-photochemical quenching were consistent with the occurrence of photoprotection under excessive irradiance levels.

Index terms: *Anacardium occidentale*, gas exchange, chlorophyll fluorescence, temperature, vapor-pressure deficit.

Respostas da fotossíntese à variação das condições ambientais em plantas jovens de cajueiro

Resumo – O objetivo deste trabalho foi caracterizar as respostas das trocas gasosas de plantas jovens de cajueiro à densidade de fluxo de fótons fotossintético (DFFF), temperatura, déficit de pressão de vapor (DPV) e concentração interna de CO₂ (C_i), sob condições controladas. Cursos diários das trocas gasosas e de variáveis de fluorescência da clorofila a foram obtidos sob condições naturais. A taxa de assimilação de CO₂ máxima foi de cerca de 13 mmol m⁻² s⁻¹, com saturação pela luz em torno de 1.000 mmol m⁻² s⁻¹. As temperaturas das folhas entre 25°C e 35°C corresponderam à faixa ótima para a fotossíntese. Os estômatos mostraram-se sensíveis ao CO₂ e se fecharam com aumentos de C_i. Aumentos do DPV exerceram pequeno efeito sobre a taxa de assimilação de CO₂, com uma pequena diminuição acima de 2,5 kPa. Os estômatos, no entanto, foram fortemente afetados pelo DPV, com fechamento gradativo acima de 1,5 kPa. As condutâncias estomáticas, reduzidas em altos DPVs, foram eficientes em restringir as perdas de água pela transpiração e demonstraram adaptação da espécie a ambientes secos. Sob irradiância natural, a taxa de assimilação de CO₂ apresentou saturação no início da manhã, variando posteriormente com as variações da DFFF. Decréscimos transientes da razão F_v/F_m foram registrados em torno de 11h, o que indica a ocorrência de fotoinibição. Decréscimos da eficiência de captura da energia de excitação, decréscimos da eficiência efetiva do fotossistema II e aumentos da extinção não-fotoquímica foram consistentes com a ocorrência de fotoproteção sob irradiância excessiva.

Termos para indexação: *Anacardium occidentale*, trocas gasosas, fluorescência da clorofila, temperatura, déficit da pressão de vapor.

Introduction

Cashew (*Anacardium occidentale* L.) is a perennial tropical species native to the Brazilian Northern Coast, where they have an important economic role (Lima, 1988). The species occupies an outstanding position among tree crops, in view of the commercial value of its nuts. Commercially important orchards are also found in the Eastern and Western Coasts of Africa, Northern Australia, Fiji Islands, Hawaii and Southern Florida (Lima, 1988). In Brazil, low crop productivity has been attempted to be solved with the introduction of new commercial dwarf clones with high productivity associated to precocious production (Barros et al., 2000).

Empirical observations have shown that cashew plants may present adaptation to a relatively large ecological range (Lima, 1988), growing well in both low and medium land tropical regions (Mendes-Ferrão, 1995). The lack of information about the species is due to limited research considering physiological aspects (Marler et al., 1994). Some studies were developed in Australia, such as: Schaper & Chacko (1993), on the influence of leaf age and branch girdling on gas exchange; Schaper et al. (1996), on the effects of irrigation on gas exchange and leaf water status; and Blaikie & Chacko (1998) and Blaikie et al. (2001), on sap flow and leaf photosynthesis as affected, respectively, by soil drying and irrigation strategies. Balasimha (1991), and Palanisamy & Yadukumar (1993) have also studied the photosynthetic characteristics of adult cashew trees in India. In Brazil, research on salinity affecting nitrogen metabolism, and solute accumulation in young cashew plants have been also carried out (Viégas & Silveira, 1999; Viégas et al., 1999).

The aim of this study was to characterize the photosynthetic response of young cashew plants to variations of environmental conditions.

Material and Methods

The study was carried out on cashew plants (*Anacardium occidentale* L.), dwarf clone CP06, grown from seeds originated from plants grafted on themselves as rootstocks and provided by Embrapa Agroindústria Tropical. The seedlings were cultivated on 2.8 L pots containing silica:vermiculite (1:1) in a greenhouse situated at the Experimental Station of Instituto Agronômico, Campinas, SP, Brazil (22°54'S and 47°5'W, 674 m altitude).

Seeds were directly sown in pots, after being soaked in distilled water for 24 hours. One month after sowing, plants began to receive Hoagland and Arnon's nutritive solution (Hoagland & Arnon, 1938) twice a week, being irrigated with distilled water in the remaining days. In the first two weeks, nutritive solution was supplied in one-tenth (first week), and half (second week), of its ionic strength. Measurements were taken from three to five 45–55 day-old plants.

For evaluation of gas exchange responses, plants were transferred to a growth chamber (Conviron E15, Canada), under controlled temperature (30°C), photosynthetic photon flux density (PPFD) of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$; and air vapor-pressure deficit (VPD) of 1.5 kPa.

Measurements were taken after one hour acclimation period in the growth chamber, in completely expanded leaves, with a Portable Photosynthesis System (Li-6400, Li-Cor, USA), equipped with a red light source and a leaf chamber.

For obtaining response curves to variations of PPFD, temperature, VPD and intercellular CO_2 concentration (C_i), each one of these conditions were separately varied in the leaf chamber, by means of the suitable control provided by the equipment, while remaining conditions were fixed. Unless when varied, PPFD was fixed at 1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, temperature at 30°C, leaf-to-air vapor-pressure difference ($\text{VPD}_{\text{leaf-to-air}}$) between 1.0 and 2.0 kPa, and CO_2 was used at atmospheric concentration.

For a better adjustment and control of $\text{VPD}_{\text{leaf-to-air}}$, the leaf chamber was supplied with an air flux with known water vapor pressures from a Dew Point Generator (Li-610, Li-Cor, USA).

Obtained values of CO_2 assimilation rates, as a function of PPFD, were adjusted by the equation $A = A_{\text{max}} [1 - e^{-k(\text{PPFD} - I_c)}]$, where A is the CO_2 assimilation rate, I_c is the light compensation point, and A_{max} is the maximum assimilation rate (Prado & Moraes, 1997). The apparent quantum yield of photosynthesis (Φ) was estimated as $\Phi = (kA_{\text{max}}) e^{(kI_c)}$ (Prado & Moraes, 1997). Stomatal limitation of photosynthesis ($S\%$) was also evaluated under optimal conditions as $S\% = [(AC_i - AC_e)/AC_i]100$ (Farquhar & Sharkey, 1982), where AC_i represents the net photosynthesis, at an internal leaf CO_2 pressure of 40 Pa, and AC_e represents the net photosynthesis at an ambient external CO_2 pressure of 40 Pa.

Daily courses of gas exchange parameters were measured in plants exposed to natural conditions, in an

open area close to the greenhouse. In the day of measurements, air temperature and VPD varied, respectively, from a minimum of 17.2°C and 0.18 kPa at 6h20 to a maximum of 28.8°C and 2.14 kPa at 16h.

Gas exchange measurements were made by a LCI Portable Photosynthesis System (ADC, England), and were accompanied by chlorophyll a fluorescence measurements made by a modulated fluorometer (FMS1, Hansatech, England).

Fluorescence measurements were taken by means of the saturation pulse method (Schreiber et al., 1994) for light and 30 min-dark-adapted completely expanded leaves. The intensity and duration of the saturation light pulse were, respectively, 18,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 0.7 s.

The following parameters were assessed: the maximum quantum yield of photosystem II (PSII) [$F_v/F_m = (F_m - F_o)/F_m$], the excitation capture efficiency of PSII open centers ($F_v'/F_m' = (F_m' - F_o')/F_m'$), the effective quantum yield of PSII ($\Delta F/F_m' = (F_m' - F_s)/F_m'$), and the nonphotochemical quenching coefficient [$\text{NPQ} = (F_m - F_m')/F_m'$], where F_m and F_o are, respectively, maximum and minimum fluorescence of dark-adapted leaves; F_m' and F_s are, respectively, maximum and steady state fluorescence in the light-adapted state, and F_o' is minimum fluorescence after far-red illumination of the previously light exposed leaves (Genty et al., 1989; Schreiber et al., 1994). Relative excessive PPFD was calculated as $[(F_v/F_m - \Delta F/F_m')/(F_v/F_m)]$, according to Bilger et al. (1995).

Results and Discussion

Maximum CO_2 assimilation rates (A) of young cashew plants, under optimal temperature, and $\text{VPD}_{\text{leaf-to-air}}$ were about 13 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with light saturation of photosynthesis around 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 1), and apparent quantum yield of 0.05 $\mu\text{mol CO}_2 (\mu\text{mol photons})^{-1}$.

Under natural conditions, a maximum CO_2 assimilation rate, around 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$, was attained, indicating a possible limitation of photosynthesis by environmental factors, which were not investigated here. Nonetheless, both CO_2 assimilation rates values are within the range described for adult cashew trees in other studies. Under natural conditions, Balasimha (1991) and Palanisamy & Yadukumar (1993) reported maximum CO_2 assimilation rates of about 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while researches in Australia reported values up to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Schaper & Chacko, 1993; Schaper et al., 1996; Blaikie et al., 2001).

Under optimal conditions, the light compensation point in cashew was 28.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, a value that approaches the range of 15 to 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ presented by Larcher (1995) for tropical tree species.

Maximum CO_2 assimilation rates in young cashew were observed between 25°C and 35°C and, even at 40°C, photosynthesis in cashew was still around 50% of its maximum value (Figure 2). This optimum temperature range reveals the species adaptation to tropical climates, since tropical woody plants, in general, present optimum photosynthesis in the range 25°C–30°C, while for temperate species the optimum range is between 15°C–25°C (Fitter & Hay, 1983).

The response pattern of stomatal conductances to temperature was similar (Figure 2), which may indicate a partial stomatal control over the photosynthetic rates at different temperatures. In fact, intercellular CO_2 values presented small increases with increased temperatures (Figure 2). The concomitant analysis of g_s and C_i response curves to temperature indicates that, in the range 20°C–35°C, the increases in C_i were related to increases in g_s .

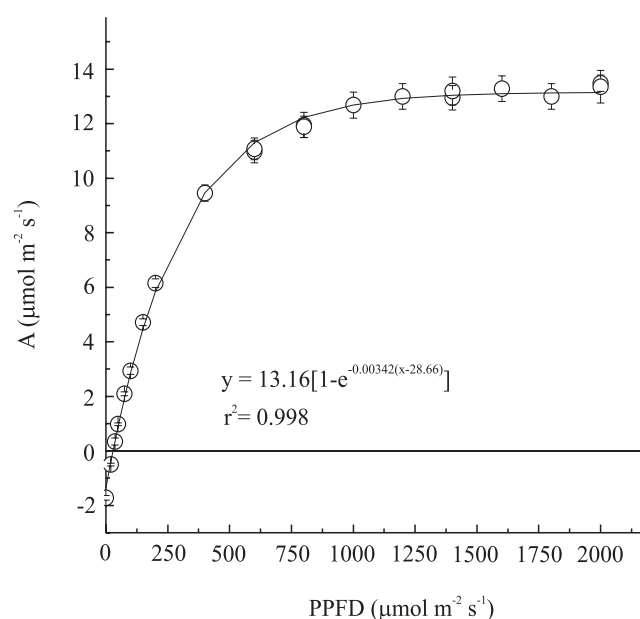


Figure 1. CO_2 assimilation rates (A) response to increasing photosynthetic photon flux density (PPFD), in young cashew plants, at 30°C leaf temperature, $\text{VPD}_{\text{leaf-to-air}}$ between 1.0 and 2.0 kPa and at atmospheric CO_2 concentration. Each point represents the mean value ($\pm\text{SE}$) of four replications taken in different plants.

Increasing stomatal opening allows a greater CO₂ diffusion to the mesophyll (Larcher, 2000), which is important to sustain high photosynthetic rates (Assmann, 1988). However, at temperatures above 35°C, decreases in g_s were accompanied by increases in C_i . Since C_i , at these temperatures, was not limiting photosynthesis, the decrease in A occurred by the interference of non-

stomatal factors (Assmann, 1998), which include the activity of carboxylation enzymes of the mesophyll. This activity can be estimated by the rate A/C_i (Zhang et al., 2001). Cashew plants showed a strong decrease of the mesophyll carboxylation activity, at temperatures above 35°C (Figure 2), indicating a loss of photosynthetic enzymatic activity. In fact, at temperatures above the

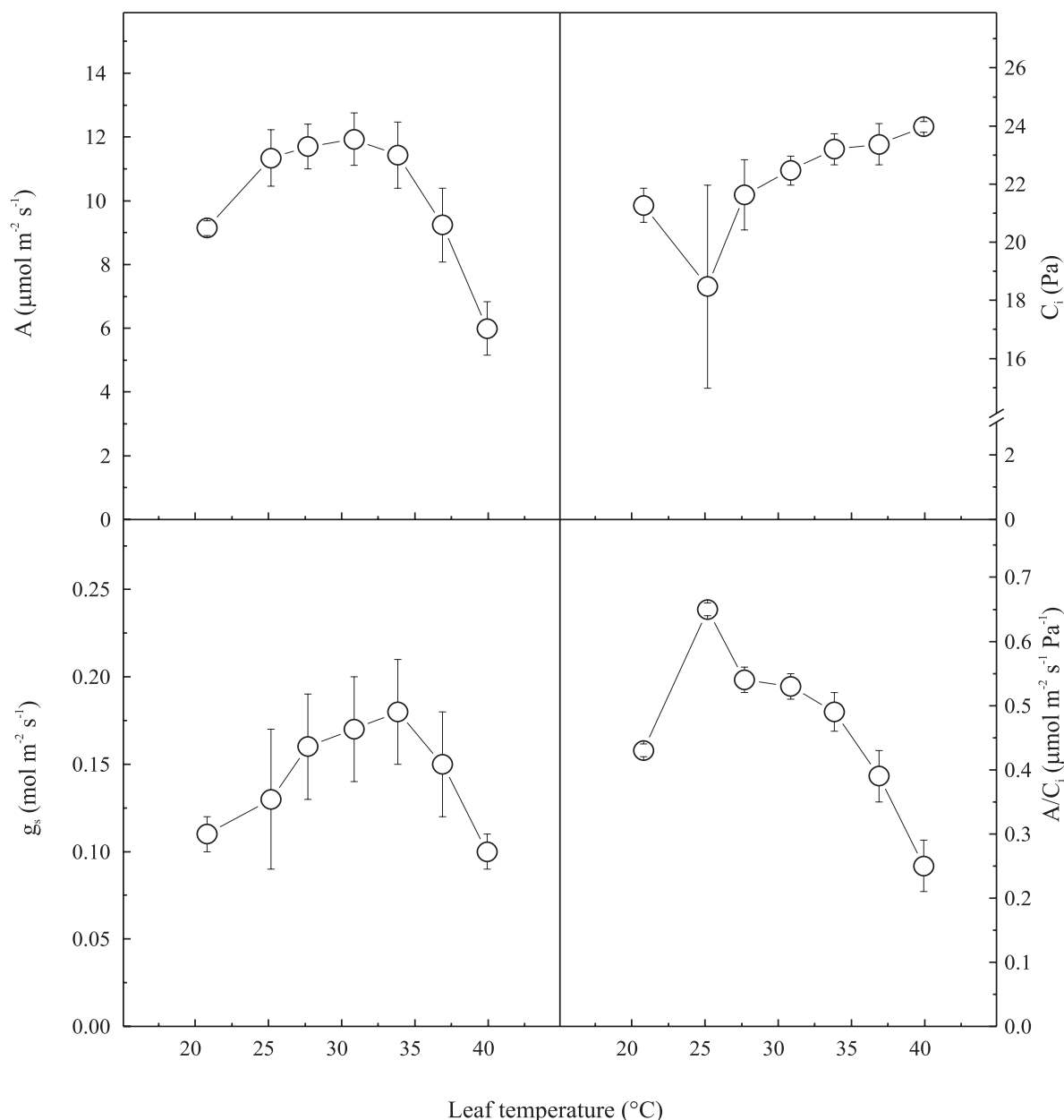


Figure 2. CO₂ assimilation rates (A), stomatal conductances (g_s), intercellular CO₂ concentrations (C_i), and mesophyll carboxylation (A/C_i) responses to increasing leaf temperature, in young cashew plants, at 1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, 1.0 kPa $\text{VPD}_{\text{leaf-to-air}}$ and at atmospheric CO₂ concentration. Each point represents the mean value (\pm SE) of three replications taken in different plants.

optimum range, the activity of Rubisco (ribulose-1,5-bisphosphate carboxylase) is affected (Weis & Berry, 1988).

The CO₂ compensation point, calculated from the assimilation response curve to intercellular CO₂ concentration, was about 6 Pa (Figure 3), a slightly lower value in relation to that reported by Balasimha (1991) for adult trees, which was between 8 and 10 Pa. The carboxylation efficiency, estimated from the same curve as its initial slope (Farquhar & Sharkey, 1982), was 0.068 $\mu\text{mol m}^{-2} \text{s}^{-1} \text{Pa}^{-1}$. Another important parameter

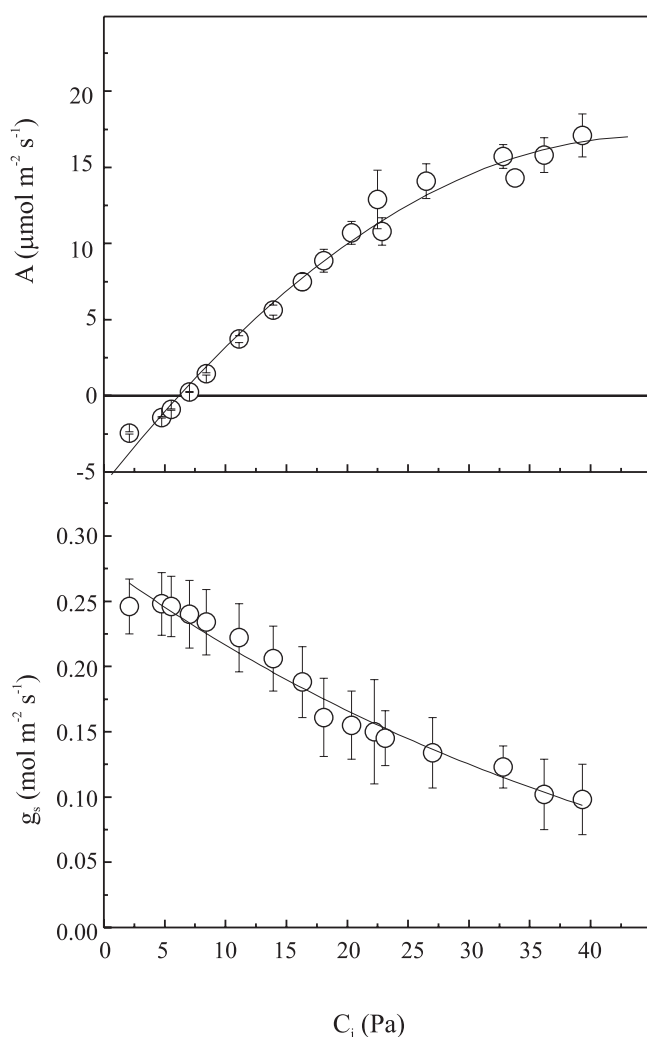


Figure 3. CO₂ assimilation rates (A) and stomatal conductances (g_s) responses to increasing intercellular CO₂ concentration (C_i), at 1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, 30°C leaf temperature, and VPD_{leaf-to-air} between 1.0 and 2.0 kPa. Each point represents the mean value (\pm SE) of four replications taken in different plants.

indicated by this curve is the limitation imposed by stomata on the photosynthesis (Farquhar & Sharkey, 1982), which in cashew plants under optimal temperature and irradiance, was of 24.6%, so that the photosynthetic capacity of mesophyll cells must contribute with more than 70% of limitation.

Stomata showed sensitivity to CO₂ with decreasing stomatal conductances when increasing intercellular CO₂ concentration (Figure 3). This kind of response can be viewed as a part of a mechanism to minimize water loss, under conditions in which CO₂ is not limiting photosynthesis (Farquhar & Sharkey, 1982). Accordingly, Eamus (1991) suggested that, under high CO₂ concentrations, reductions in stomatal conductances, associated with the higher CO₂ assimilation rates, contribute to increase water use efficiency.

Varying vapor-pressure deficits had a small effect on CO₂ assimilation rates. These rates were maintained at relatively high values in the VPD_{leaf-to-air} range, 1.0–3.5 kPa, despite small decreases above 2.5 kPa (Figure 4). Balasimha (1991) also found, for adult trees in India, that cashew photosynthesis was not substantially affected by VPD in the range 2.0–4.0 kPa. Stomata, however, were strongly affected by VPD_{leaf-to-air}, with an observed gradual closure above 1.5 kPa (Figure 4). The reduced stomatal conductances, at high VPD_{leaf-to-air}, were efficient in restricting water losses by transpiration. In the absence of any change in stomatal conductances, the ratio of transpiration, for a leaf maintained at constant temperature, is expected to be directly proportional to VPD (Morison & Gifford, 1983). However, in cashew plants, transpiration rates were kept constant over the range 2.0–3.5 kPa (Figure 4), due to the stomatal closure. Internal CO₂ was little affected by stomatal closure, which can explain the maintenance of high CO₂ assimilation rates, at relatively high VPD_{leaf-to-air}. In general, the response of cashew plants to increasing VPD_{leaf-to-air} may demonstrate some adaptability to dry environments, since plants can maintain relatively high photosynthetic activity, under conditions of accentuated vapor-pressure deficits.

Daily courses of photosynthetic activity demonstrated that CO₂ assimilation rates were saturated in early morning, following thereafter the PPFD changes (Figure 5). The decrease of PPFD around midday, because of the presence of clouds, was accompanied by decreases in CO₂ assimilation rates and stomatal conductance (Figure 5).

Blaikie & Chacko (1998) showed that gas exchange was closely related to fluctuation in stomatal

conductances, with these values generally being lower in the afternoon than in the morning. These observations are also valid for this study, since curves of CO_2 assimilation rates and stomatal conductances varied similarly during the day. Transpiration rates were greater in the afternoon, reaching a peak around 14h (Figure 5).

The maximum quantum yield of PSII, as assessed by F_v/F_m ratio, was optimum in early morning (around 0.8), decreasing to a minimum value (around 0.6) at 11h. A small recovery began to occur during the afternoon (Figure 6). Small decreases of F_v/F_m ratio during the day were also observed by Blaikie & Chacko (1998),

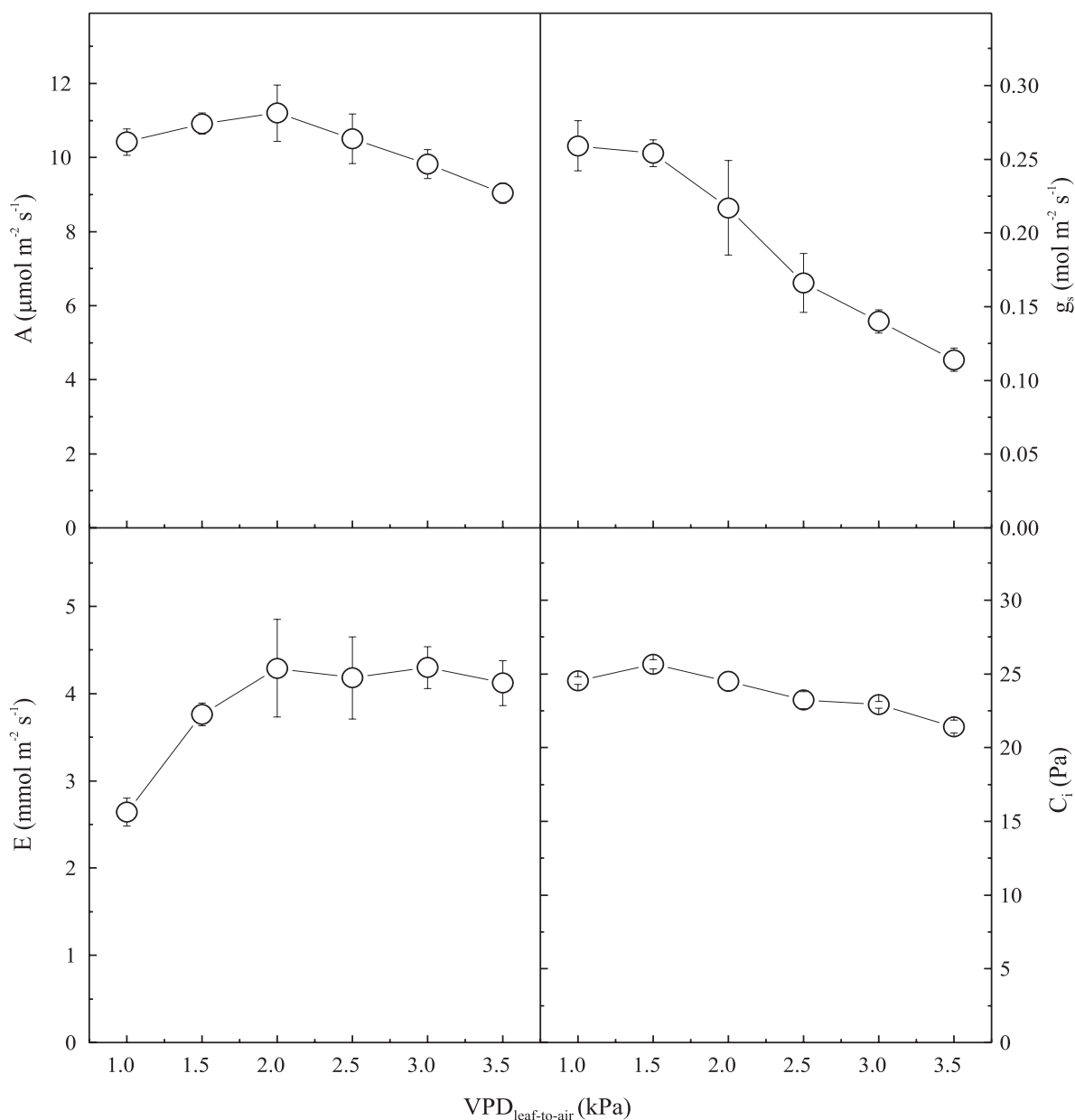


Figure 4. CO_2 assimilation rates (A), stomatal conductances (g_s), transpiration rates (E), and intercellular CO_2 concentration (C_i) responses to increasing $\text{VPD}_{\text{leaf-to-air}}$ in young cashew plants at $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, 30°C leaf temperature and at atmospheric CO_2 concentration. Each point represents the mean value ($\pm\text{SE}$) of five replications taken in different plants.

indicating photoinhibition of photosynthesis in cashew plants (Bolh ar-Nordenkamp &  quist, 1993). This phenomenon occurs when the amount of energy, intercepted by photosynthetic apparatus, exceeds the capacity of its utilization in photochemical reactions (Krause, 1988).

F_v/F_m decreases may be either the result of some photosynthetic damage or photoprotective mechanisms (Osmond, 1994). Although the distinction between photoprotection and photodamage is not always clear, protective photoinhibition is recognized by a rapid recovery of F_v/F_m ratio after a dark adaptation period.

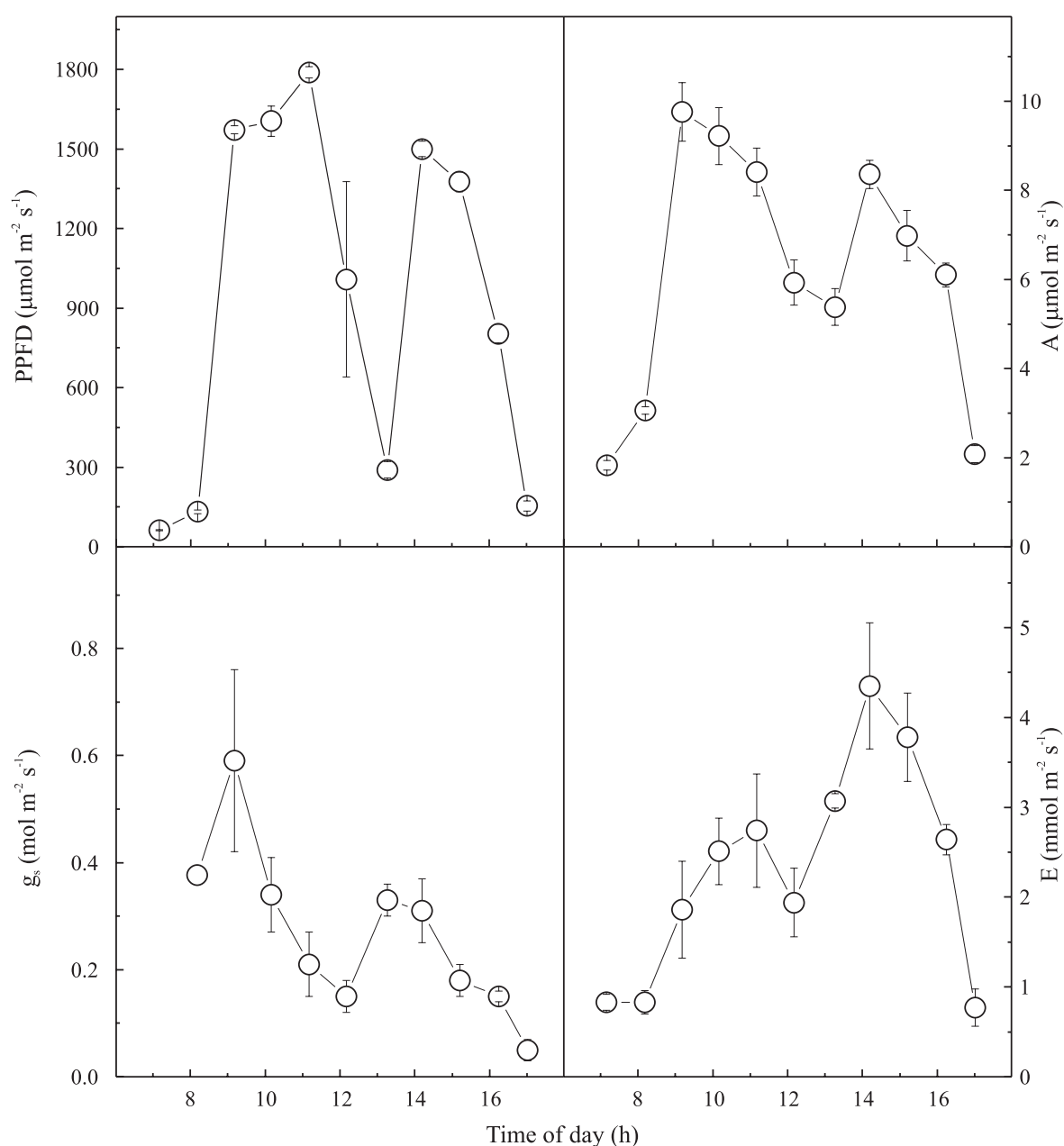


Figure 5. Daily courses of photosynthetic photon flux density (PPFD) and associated CO_2 assimilation rates (A), stomatal conductances (g_s) and transpiration rate (E), in young cashew plants. Each point represents the mean value ($\pm\text{SE}$) of five replications taken in different plants.

It may involve changes in PSII antenna, which favors the dissipation of excess energy as heat (Osmond, 1994). In cashew plants, F_v/F_m decrease was only transient, showing a slight recovery during afternoon, and a complete overnight recovery, since morning values were

always in the optimum range. These results indicate that, at least, no permanent PSII damage occurred.

The decrease in the excitation capture efficiency of PSII (Figure 6) is consistent with the occurrence of photoprotection, as well as the observed increases in non-

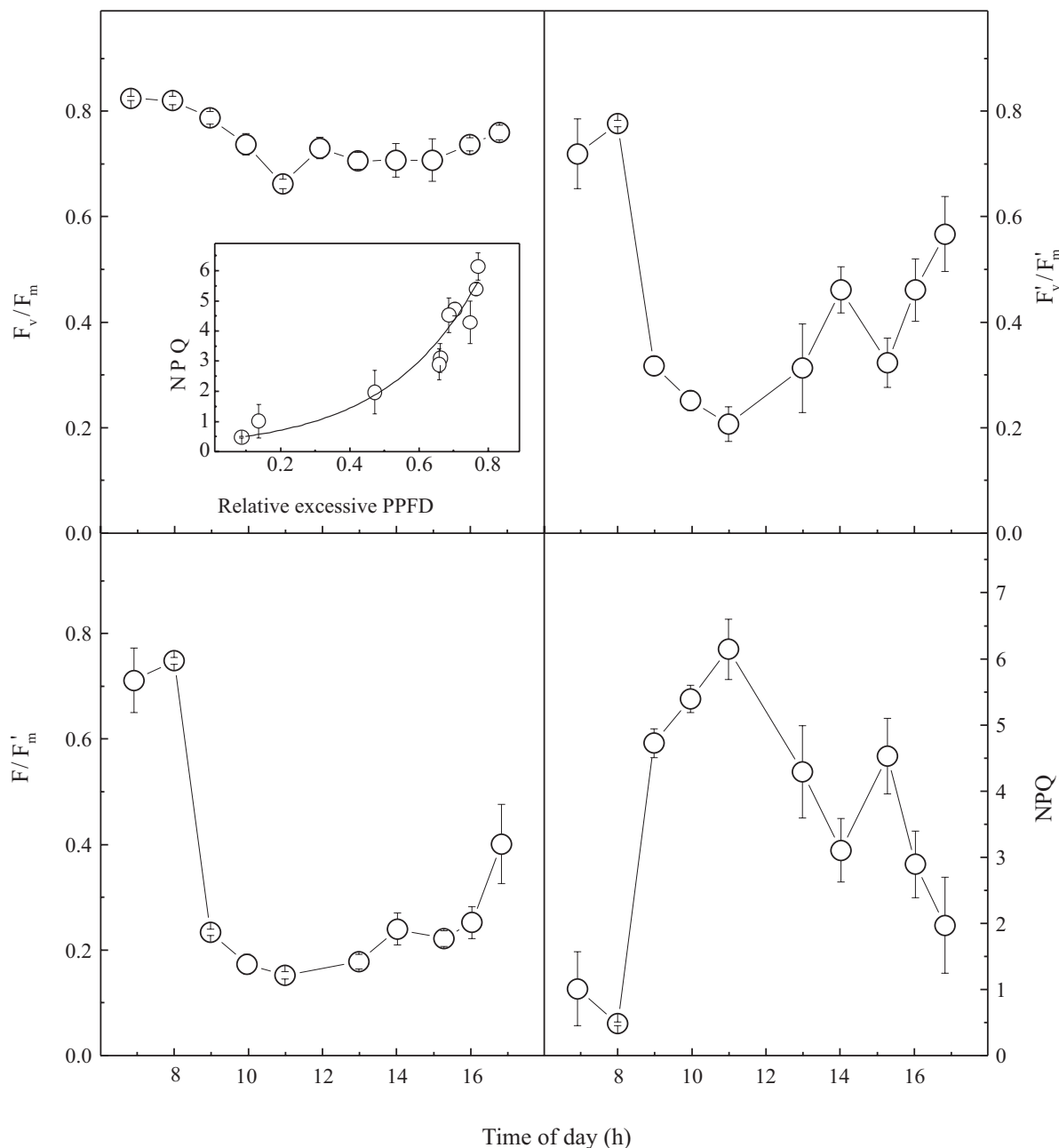


Figure 6. Daily courses of chlorophyll a fluorescence parameters, in young cashew plants under natural conditions, showing maximum quantum yield of PSII (F_v/F_m), excitation capture efficiency by PSII open centers (F_v'/F_m'), effective quantum yield of PSII ($\Delta F/F_m'$), nonphotochemical quenching coefficient (NPQ), and NPQ as function of the relative excessive photosynthetic photon flux density (PPFD). Each point represents the mean value (\pm SE) of five replications taken in different plants.

photochemical quenching during the day, particularly around 11h, and under increased relative excessive PPFD.

As a consequence, the values of effective quantum yield of PSII, that were high in early morning, decreased to 0.2 and remained at low values until 16h. Here again, these values of effective quantum yield were similar to those reported in other studies (Blaikie & Chacko, 1998; Blaikie et al., 2001). Since no damages to the photosynthetic system were evident, the photoinhibition in young cashew plants was effective in protecting the photochemical apparatus, at the high irradiance levels, to which plants were exposed in their natural environments.

Conclusions

1. Leaf temperatures, between 25°C and 35°C, are optimal for photosynthesis in young cashew plants, revealing the species adaptation to tropical climates.

2. Under high vapor-pressure deficits, stomatal closure of young cashew plants can be efficient in restricting water losses by transpiration.

3. Young cashew plants can maintain relatively high photosynthetic activity, under conditions of accentuated vapor-pressure deficits, which associated with the stomatal response pattern, can be considered an species adaptation to dry environments.

4. Under natural conditions of high irradiance, young cashew plants show photoinhibition of photosynthesis, protecting the photosynthetic apparatus from permanent photodamage.

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