Photosynthetic Photon Flux Density, Carbon Dioxide Concentration and Temperature Influence Photosynthesis in C*rotalaria* Species

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Abstract: Crotalarias are tropical legumes grown as cover crops or as green manure to improve soil fertility. As an understory plant in plantation systems, these cover crops receive low levels of irradiance and are subjected to elevated levels of CO_2 and temperatures. A greenhouse experiment was conducted to evaluate the independent short-term effects of photosynthetic photon flux density (PPFD), external carbon dioxide concentration (C_a) and temperature (T) on net photosynthesis (P_N), internal CO_2 (C_i), stomatal conductance (g_s) and transpiration (E) in four *Crotalaria* species (*C. breviflora, C. mucronata, C. ochroleuca, C. spectabilis*). These crotalarias responded differently to changing PPFD, C_a and T. In all the *Crotalaria* species, increasing PPFD from 50 to 1500 µmol m^{-2} s^{-1} increased P_N by 21 fold, increased g_s by 2.3 fold (136%), decreased C_i by 3.9 times, and increased E by 2.1 times. Increasing the external C_a from 100 to 1000 cm^3 m^{-3} increased P_N by 4.7 fold, decreased g_s by 1.3 times, increased C_i by 28 fold, and decreased E by 1.2 times. Increasing the T from 25 to 35 °C increased P_N of *Crotalaria* species by 11%, decreased g_s by 33%, decreased C_i by 64%, and increased E by 56%. Shade management is critical to maintaining the productivity of these tropical legumes.

Keywords: Leaf internal CO_2 concentration, net photosynthesis, stomatal conductance, *Crotalaria* spp, transpiration rate.

INTRODUCTION

Perennial legumes are grown as green manure crops or as non-understory or understory cover crops in tropical regions in row crops or in plantation systems [1]. Legume cover crops improve soil fertility by fixing atmospheric N_2, increasing soil organic matter content and soil aggregation, enhancing water holding capacity and improving biological activity [1, 2]. They also reduce soil erosion, leaching and run-off losses of nutrients, and decrease weeds, diseases and pest infestations [1-3]. Various crotalaria species are grown in tropical regions as green manure crops, in fast growing row field crops or as understory cover crops in perennial plantation systems [4, 5]. Crotalarias are fast-growing green manure or cover crops that can yield 5 to 10 t/ha/yr of dry matter, fix 60-200 kg/ha/yr of nitrogen and improve soil quality components [1, 4, 6]. However, they have limited use as forage crops because they produce animal toxicity (pyrrolizidine alkaloids) [7].

Cover crops grown as understory plants in plantation systems receive very limited irradiance [8, 9]. In addition to the global increase in C_a [10], increased litter decomposition in plantation systems contributes additional CO_2 at the canopy level. However information is lacking how these climatic variables affect the growth and physiological traits of crotalarias. Survivability and persistence of understory cover crops depends largely on the rate of P_N, and this is affected by the amount and quality of light that reaches the cover crop canopies [9, 11]. In tropical regions incoming photosynthetic active radiation (PAR) is around 1800 µmol m^{-2} s^{-1} [12], but understory plants in rainforests receive only 4 to 10% of this radiation [8, 13]. Shading reduces yields of most tropical legumes [9, 11, 14, 15]. Legume cover crops having greater tolerance to low light (high shade) intensity offer considerable promise by increasing their growth and persistence as understory plants in perennial plantations. Existence of inter-/intra-specific differences in shade tolerance in tropical cover crops/forage legumes have been reported [14, 16-20]. However the ability of crotalarias to grow at low PPFD is unknown. The P_N in *Crotalaria brevidens* increased rapidly with increasing irradiance to 1000 µmol m^{-2} s^{-1} and increased gradually with further increases in irradiance to 2000 µmol m^{-2} s^{-1} [21].

The carbon dioxide concentration (C_a) in the atmosphere has risen from 280 cm^3 m^{-3} in 1900 to present day levels of around 390 cm^3 $m^{-3}$and is expected to approach 700 cm^3 m^{-3} by the end of the 21st century [10]. Litter decomposition in plantation crops contributes additional C_a at ground level. Elevated C_a also contributes to increased plant biomass and enhanced P_N [22-24]. Therefore, rising concentrations of atmospheric C_a could increase P_N per unit leaf area of C3 plants. However, in many species, such an increase in P_N is often reduced after prolonged exposure to elevated C_a [25, 26]. Increases in C_a increased the growth of many C_3 plants [27]; however, growth is usually not as large as would be predicted simply from the increase in photosynthesis [28-30]. Elevated C_a increases plant biomass by increasing P_N and water use efficiency (WUE) and by decreasing transpiration rate (E) through reduced stomatal conductance [24, 30]. Doubling atmospheric C_a reduced stomatal

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conductance in C3 annual crop plants by 34% [25]. Such phenomena have been documented in other plant species [25, 32]. Vu [33] reported that peanut (*Arachis hypogaea* L.) leaves grown under elevated C_a (720 µmol mol^{-1}) had higher midday photosynthetic CO_2 exchange rates (CER), lower transpiration and higher WUE, than leaves grown under at ambient C_a (360 µmol mol^{-1}). In an evergreen forest, stomatal conductance is an important limiting factor for photosynthetic responses of understory plants to sunflecks [34]. Sunflecks account for 40% or more of the total daily photon flux density received by understory plants in evergreen forests, and high C_a might allow understory plants to exploit sunflecks more efficiently [35, 36].

It has been projected that global surface temperature is likely to increase by 5.8 ºC by the end of this century due to increases in tracer gases, including CO_2 [37, 38]. In legumes, radiation use efficiency is profoundly influenced by ambient temperature [39, 40]. Studies on elevated C_a and temperature effects on P_N have been primarily reported for temperate, annual legume species [22-25, 33]. Recently, Baligar *et al.*, [41] in a short term study reported that by increasing ambient temperature from 30 ºC to 35 ºC differential responses of P_N were observed in tropical perennial legumes. In this study, increasing temperature reduced P_N in these legumes. Information is lacking on the effects of increased atmospheric [CO_2], increased temperature, and reduced light on P_N of understory perennial legumes. Crotalarias are grown in a temperature range of 16 to 26 ºC [3] and are known to tolerate temperatures as low as 12ºC and as high as 35ºC [1]; however, the optimal temperature range for P_N in many of the tropical cover crops is not well documented. Canopy temperature of understory plants is less than plants under no shade [42]. High temperature often reduces growth and biomass by decreasing photosynthesis and increasing E [43]. In peanut, leaf water potential, hydraulic conductivity (gh), transpiration rate (E) and stomatal conductance (g_s) increased with increasing soil temperature [40]. Imbamba and Tieszen [21] reported that P_N in *Crotalaria brevidens* decreased with increases in leaf temperature from 10 to 50°C. However the rate of transpiration increased with increasing leaf temperature. Leaf diffusive resistance decreased with increasing irradiance but increased with increasing leaf temperature [21].

The objectives of the current study were to evaluate the independent short-term effects of photosynthetic photon flux density (PPFD), external carbon dioxide concentration (C_a) and temperature (T) on net photosynthesis (P_N) and photosynthetic components (g_s, E, C_i) in four crotalaria species: *Crotalaria breviflora*, *C. mucronata*, *C. ochroleuca*, and *C. spectabilis*.

MATERIALS AND METHODS

Crotalarias Used and Growth Conditions

Cover crops selected for study were: Showy Croalaria (*Crotalaria spectabilis* Roth), Short Flowered Crotalaria (*Crotalaria breviflora* DC.), Smooth Crotalaria (*Crotalaria pallida* Aiton/ *mucronata* Desv.), Rattlebox (*Crotalaria ochroleuca* G. Don). Crotalaria belongs to the *Fabaceae* (*Leguminosae/Papilionace*) family and genus *Crotalaria* [44]. Showy Crotalaria is an annual/perennial non climbing herb/shrub with potential for soil erosion control and known improver of soil. Short Flowered Crotalaria is a perennial non climbing herb/shrub and known improver of soil quality parameters. Smooth Crotolaria is annual/perennial non climbing herb and is a known improver of soil quality parameters. Rattlebox Crotalaria is an annual/perennial, erect/semi-erect non climbing herb/shrub [6, 45]. Seeds of various crotalarias were obtained from Pirai Seed Company, Av. Cassio Paschoal Pado.Vam; No 333, Piracicaba-SP Brazil.

Plants were grown in plastic pots containing 2 kg of 2:2:1 mixture of Sand: Perlite: Peat moss medium (pH 5.0) and supplemented with all the essential nutrients (mg/kg) of 600 N, 600 P, 240 K, 1012 C, 309 Mg, 500 S, 119 Fe, 0.7 B, 17.5 Mn, 7 Cu, 7 Zn and 0.35 Mo. Nutrients were applied as Osmocote (18-6-12; Scotts, Marysville, Ohio), triple super phosphate, urea, calcium sulphate, dolomitic lime, and Scott's micromix. During growth soil moisture was maintained near field capacity (33 kPa). Plants were grown for 36 days in a greenhouse under 400±50 µmol m^{-2} s^{-1} of PPFD for 12 h, 370±30 cm^3 m^{-3} of carbon dioxide and day and night temperatures of 32±5°C and 15±5°C, respectively.

Determination of Net Photosynthesis and Its Components (C_i, g_s, E)

On the 34th day of growth, plants were moved to a controlled environment chamber with 400 µmol m^{-2} s^{-1} of irradiance (PPFD) for 12 h, 370±30 cm^3 m^{-3} of C_a and a constant temperature of 25°C. After two days in the growth chamber, 3 plants per species were subjected to photosynthetic determinations. Photosynthesis was measured on the third leaf from the top of each plant using a CIRAS-2 portable gas exchange system (PP Systems, Haverhill, MA, USA) with a 2.5 cm^2 leaf chamber. The air flow rate was 200 cm^3 s^{-1}. PPFD was supplied by the CIRAS LED light source. Temperature was controlled by peltier elements on the leaf chamber unit. [CO_2] was controlled by the CIRAS-2 instrument.

Experiment I: Effect of Light [PPFD] Intensity

The third leaf was placed in the cuvette of the CIRAS-2 system and adjusted to conditions of PPFD of 1500 µmol m^{-2} s^{-1}, T of 30°C, C_a of 400 cm^3 m^{-3} and VPD (vapor pressure deficit) of 2.0-2.5 kPa. After the leaf gas exchange became constant, the PPFD was adjusted in gradual steps to 1000, 500, 300, 100, 50 µmol $m^{-2}s^{-1}$. The leaf was allowed to equilibrate at the chosen PPFD for 10 min and P_N and its components C_i, g_s, E were determined.

Experiment II: Effect of Carbon Dioxide Concentration (C_a)

The third leaf was placed in the cuvette with PPFD of 1500 µmol m^{-2} s^{-1}, VPD of 2.0-2.5 kPa, and temperature of 30°C. The carbon dioxide concentration was initially adjusted to 400 cm^3 m^{-3}. After the leaf gas exchange became constant, the C_a was adjusted in gradual steps to 100, 250, 700 and 1000 cm^3 m^{-3}. The leaf was allowed to equilibrate at the chosen C_a for 10 min and P_N and its components C_i, g_s, E were determined.

Experiment III: Effect of Temperature (T)

The third leaf was placed in the cuvette and leaf temperature was adjusted to 25°C with PPFD of 1500 µmol m^{-2} s^{-1}, C_a at 400 cm^3 m^{-3} and the VPD at 2.0-2.5 kPa. After

the leaf gas exchange became constant, the temperature was adjusted in gradual steps to 28, 30, and 35°C. The leaf was allowed to equilibrate at the chosen temperature for 10 min and P_N and its components C_i, g_s, E were determined. In this experiment, VPD increased with temperature, with mean values of 1.71, 2.15, 2.57, 3.66 kPa at 25, 28, 30 and 35°C, respectively.

Statistics

Standard deviation of data points of various measurements of each leaf were determined by SigmaPlot Ver. 10 and values were plotted on the graphs.

RESULTS AND DISCUSSION

PPFD Effects

In all species, increasing PPFD from 50 to 1500 μmol m^{-2} s^{-1} increased P_N (Fig. **1A**). Overall, there was a 21 fold increase in P_N from 50 to 1500 μmol m^{-2} s^{-1} of PPFD, and P_N continued its upward trend at 1500 μmol m^{-2} s^{-1} suggesting that it had not reached irradiance saturation. P_N values among four crotalaria species converged as the PPFD decreased but were divergent at 1500 μmol m^{-2} s^{-1} of PPFD. Baligar *et al.,* [41] reported a similar trend in effects of varying PPFD on P_N of five tropical perennial legumes. PPFD of 500 μmol m^{-2} s^{-1} gave 66% of the maximum P_N at 1500 μmol m^{-2} s^{-1}. *C. breviflora* and *C. ochroleuca* were always higher than *C. mucronata* and *C. spectabilis.* Imbamba and Tieszen [21] reported that P_N in *C. brevidens* increased with increases in PPFD up to 1000 μmol m^{-2} s^{-1} and increased gradually with further increases in PPFD to 2000 μmol m^{-2} s^{-1}. Crotalaria species used in our study were very sensitive to low irradiance confirming the observations of Ludlow and Wilson [46] and Wilson and Ludlow [47] that P_N of understory legumes is influenced by the amount of radiation reaching the crop canopy. Soils receive full sunlight early during establishment of tree crops either in an agroforestry system or non agroforestry system, but the amount of light that reaches the soil is drastically reduced as the trees grow. Miyaji *et al*., [8] reported that in Bahia, Brazil, above the canopy of shaded and non shaded cacao the light intensity ranged from 600 to 2000 μmol m^{-2} s^{-1} and at ground level the light intensity was 80 to 200 μmol m^{-2} s^{-1}. Our results indicate that all four crotalarias species would photosynthesize adequately in newly established plantations. However, growth would be reduced dramatically as the trees matured and incident light levels fell below 500 μmol m^{-2} s^{-1}. This confirms the notion that legume cover crops do well in early stages of tree fruit crops establishment, such as cacao, due to availability of high light intensity. However, as the trees mature, the growth, persistence and effectiveness of cover crops are reduced owing to low light intensity.

P_N recorded at higher PPFD is comparable to those reported for temperate and tropical legumes [30, 47]. At all levels of PPFD, *C. breviflora* and *C. ochroleuca* produced higher P_N than the other two crotalarias, indicating that these two grow well under no shade or moderate shade. Inter-/intra specific differences in shade tolerance of tropical legumes has been widely reported [14, 16, 17, 41, 48, 49]. Information is lacking on the response of crotalarias to shade in plantation crop systems. Crotalarias that tolerate lower PPFD have a better chance of growing as understory plants and protecting soil longer in plantation crop systems. To make crotalarias more productive and efficient as cover crops in plantation agriculture, it is essential to manage canopies of associated shade trees to reduce excess shading.

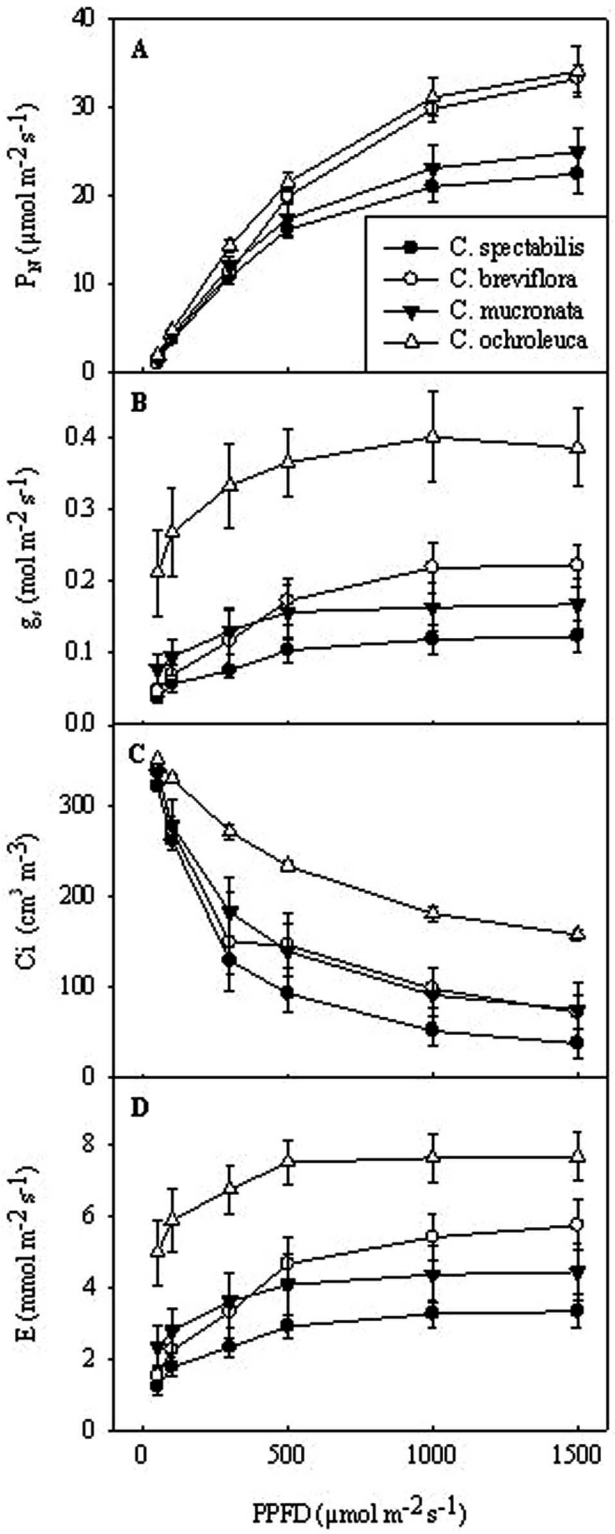

Fig. (1). Effect of PPFD levels on (**A**) net photosynthetic rate, P_N; (**B**) stomatal conductance, g_s; (**C**) internal CO_2 concentration, C_i; and (**D**) transpiration rate, E, of four Crotalaria genotypes at T of 30 °C and C_a of 400 cm^3 m^{-3}. Each symbol represents the average of three reps.

In understory plants, stomatal conductance (g_s) sometimes plays a vital role in regulating P_N. Increasing g_s with increasing PPFD is necessary to support higher P_N (Fig. **1B**). Crotalarias having high P_N showed significantly higher g_s at all the PPFD rates evaluated. In all crotalarias, g_s increased up to 500 µmol m^{-2} s^{-1} of PPFD then remained fairly constant with further increases in PPFD. High g_s due to wide stomatal openings increases water loss through transpiration, which can be detrimental by inducing water stress in low rainfall situations. *C. ochroleuca* at all the PPFD had 3 to 4 times higher g_s than other crotalarias indicating that this crotalaria is potentially very susceptible to drought stress.

Internal CO_2 (Ci) decreased as the PPFD increased for all crotalaria species (Fig. **1C**). This is expected because higher irradiance levels increase P_N, using more of the available internal CO_2 thereby giving an inverse relationship between the two. Transpiration (E) followed a pattern similar to that of g_s (Fig. **1D**).

C_a Effects

Increasing the external CO_2 concentration from 100 to 1000 cm^3 m^{-3} increased P_N of crotalaria species by 5 fold. Increasing C_a from 400 to 700 cm^3 m^{-3} increased P_N by 1.4 times (Fig. **2A**). In C3 plants, Kimball [50] and Drake and Leadley [26] reported that high atmospheric [CO_2] increased P_N rates and decreased g_s and E. In our study P_N response in all four crotalarias suggests that increasing atmospheric [CO_2] will have beneficial effects on P_N thereby improving their growth and persistence at an adequate PPFD. If anticipated global C_a of 700 cm^3 m^{-3} by the end of 21st century are realized [10], these crotalaria species would respond well to the new conditions in tropical plantations. The findings in this study of a positive response of P_N with increasing C_a confirm the findings of Bhagsari and Brown [51] and Baligar *et al.*, [41]. Higher C_a might allow the understory plants to use sunflecks more efficiently. Sunflecks accounted for 40% or more of daily photon flux density received by understory plants in evergreen forests [35, 36].

Increases in C_a from 100 to 1000 cm^3 m^{-3} decreased g_s (Fig. **2B**) and E (Fig. **2D**), depending on species. For *C. spectabilis* and *C. mucronata*, g_s decreased 1.5 and 2.6 times, respectively, while *C. breviflora* and *C. ochroleuca* remained relatively constant. E followed patterns similar to those of g_s. It has been widely reported that in most plants, elevated C_a decreased evapotranspiration through reduction of g_s [24, 26, 31, 50]. However, Baligar *et al.*, [41] reported the reduction of g_s and E in only one tropical legume (*Leucaena leucocephala*) with increasing C_a.

Internal CO_2 (Ci) increased as external [CO_2] increased from 100 to 1000 cm^3 m^{-3} (Fig. **2C**). The exception was *C. mucronata* in which Ci increased with increased C_a up to 700 cm^3 m^{-3} and leveled off with further increases in C_a.

T Effects

Globally, it has been projected that, by the end of this century, surface temperature will increase by 5.8 °C [37, 38], and such an increase in temperature might have considerable influence on the P_N and its components in understory plants.

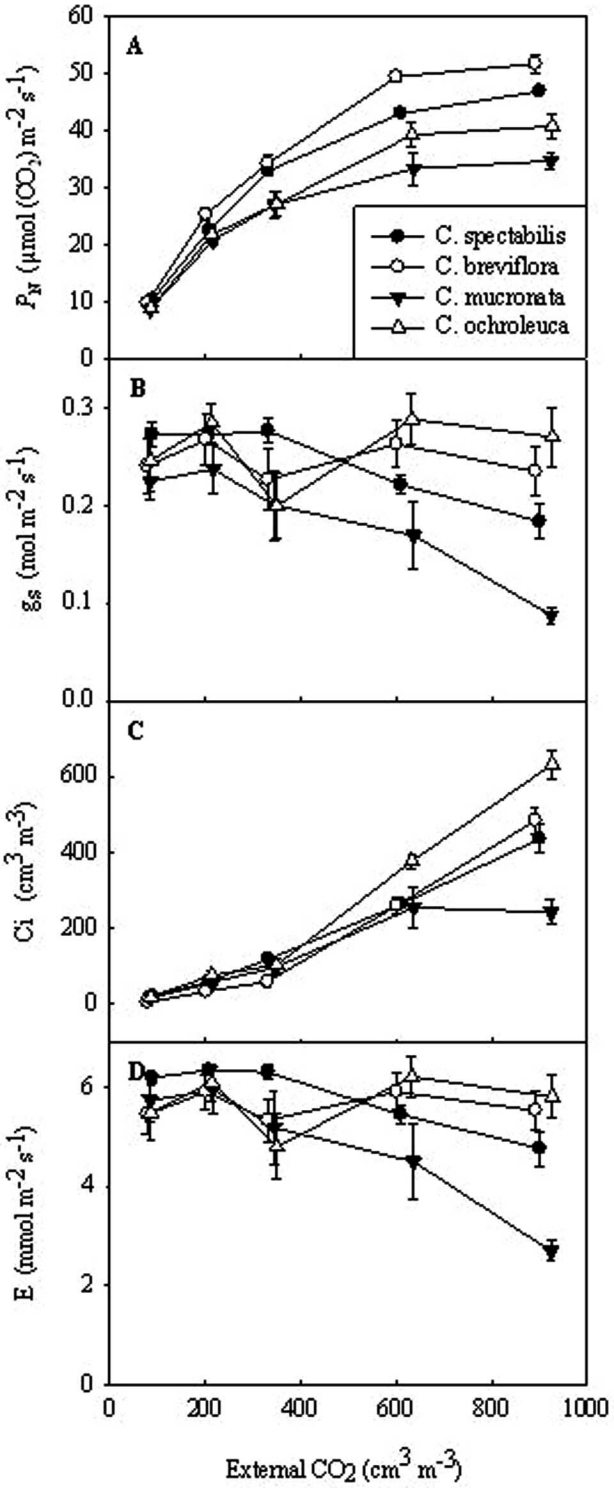

Fig. (2). Effect of external C_a levels on (**A**) net photosynthetic rate, P_N; (**B**) stomatal conductance, g_s; (**C**) internal CO_2 concentration, C_i; and (**D**) transpiration rate, E of four Crotalaria genotypes at T of 30 °C and PPFD of 1500 µmol m^{-2} sec^{-1}. Each symbol represents the average of three reps.

Shade from the overstory trees reduces warming of the soil and air above the canopy of understory plants [42, 47]. Temperature optima for many tropical legumes have been reported in the range of 15 to 35°C [52-54]. In our study,

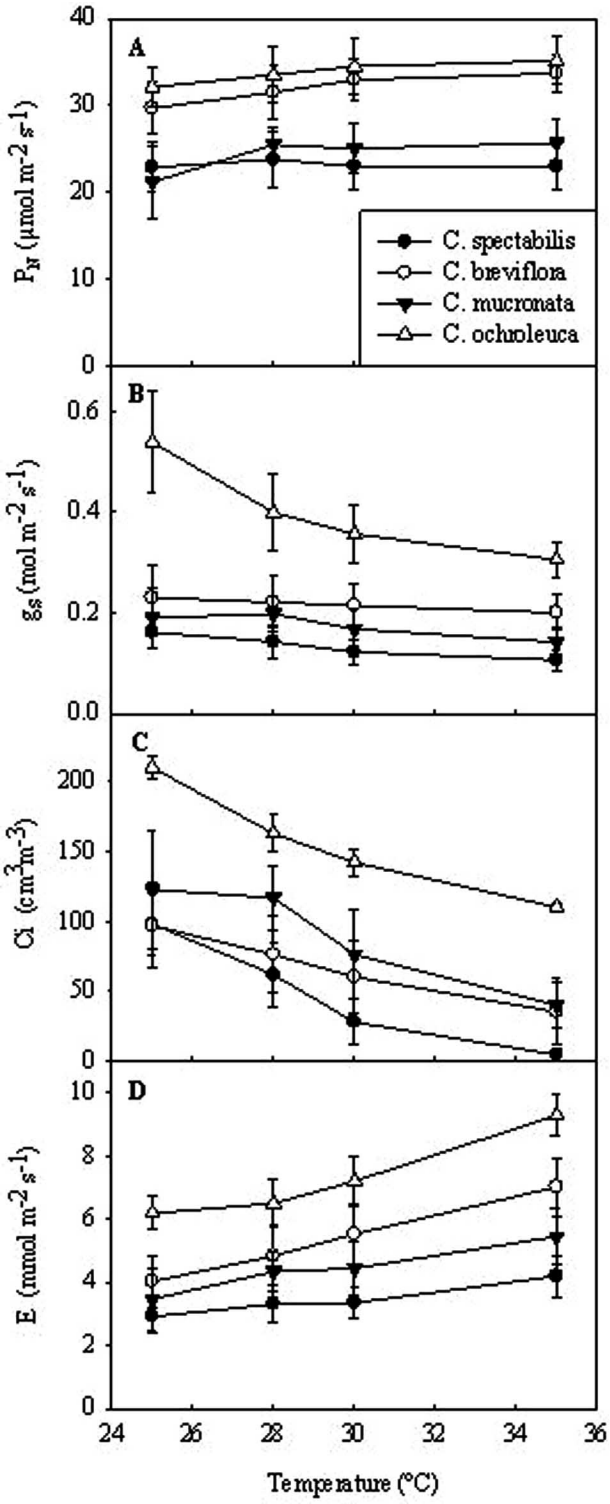

Fig. (3). Effect of temperature on (**A**) net photosynthetic rate, P_N; (**B**) stomatal conductance, g_s; (**C**) internal CO_2 concentration, C_i; and (**D**) transpiration rate, E of four Crotalaria genotypes at PPFD of 1500 µmol m^{-2} sec^{-1} and C_a of 400 cm^3 m^{-3}. Each symbol represents the average of three reps.

increasing temperatures in the range of 25 to 35°C had little effect on P_N of the four crotalaria species (Fig. **3A**). These findings differ with those of Imbamba and Tieszen [21] who reported that P_N in *C. brevidens* decreased with increasing leaf temperature from 10 to 50 °C. The observed P_N values in the current study are different from those of many temperate, annual legume species as well, where P_N began to decrease with increasing temperature [22, 33, 39, 40]. Baligar *et al*., [41] recently reported that increasing temperature from 30 to 35°C reduced P_N in several tropical cover crop legumes. Differences in P_N values obtained in the current study are not in agreement with those other literature values and are probably due to differences in leaf residence time used to measure P_N at various temperatures. Longer exposure of leaves to various temperatures might have given different values for P_N.

With the exception of *C ochroleluca*, stomatal conductance (g_s) remained constant over the range of 25 to 35°C for *C. breviflora*, *C. spectabilis* and *C. mucronata* (Fig. **3B**). The g_s of *C. ochroleuca* decreased 1.8 times from 25 to 35°C. In all four crotalaria species studied, Ci declined rapidly with increasing temperature and was inversely related to P_N (Fig. **3C**). Internal CO_2 (Ci) decreased by an average of 2.8 times from 25 to 35 °C. Transpiration (E) in all crotalaria species increased by an average of 1.5 times from 25 to 35°C (Fig. **3D**), partly because of the increase in VPD with temperature. These findings support the earlier report of Imbama and Tieszen [21] with *C. brevidens*. In low rainfall areas or in drought conditions increasing ambient temperatures could induce water stress in crotalaria species. However increasing temperature had no effect on g_s and this could reduce the loss of water from leaves.

CONCLUSIONS

This study has clearly demonstrated that increasing light intensity and carbon dioxide enhanced photosynthesis in all of the crotalaria species. Increasing temperature from 25 to 35 °C had little effect on P_N of crotalaria. Shade management of overstory trees is essential to maintain the persistence and productivity of crotalaria species in tree plantations.

CONFLICT OF INTEREST

Declared none.

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