

Irradiance, external carbon dioxide concentration and temperature influence photosynthesis in tropical cover crop legumes

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Abstract

In plantation crops, perennial tropical legumes are grown as understory plants, where they receive limited irradiance and can be subjected to elevated levels of CO₂. Independent short-term effects of photosynthetic photon flux density (PPFD), external carbon dioxide concentration [CO₂] and temperature on net photosynthesis (Pn), internal CO₂ (Ci), stomatal conductance (Gs) and transpiration (E) were assessed in 5 tropical perennial legume cover crops (calopo, jack bean, mucuna, white lead tree and perennial peanut). These legumes responded differently to changing PPFD, external [CO₂] and temperature. In all legume species studied, reducing PPFD from 1000 to 50 μmol/m²/s reduced Pn to less than 10% of that at the higher light level. Increasing the external [CO₂] from 250 to 700 cm³/m³ doubled Pn. Increasing temperature from 30°C to 35°C reduced Pn in calopo, jack bean and mucuna and increased Pn in white lead tree and perennial peanut, but magnitude of the differences was small. Gs increased with PPFD in all species except perennial peanut, but decreased substantially as external [CO₂] increased only in white lead tree. Early in the establishment of plantations, soils receive nearly full sunlight. However, with increasing age, the amount of light reaching ground level is decreased drastically, to as low as 80–200 μmol/m²/s. Cover crops that can grow in low light might survive longer and better protect

the soil from erosion. Responses of these perennial legumes under the conditions imposed have shown that white lead tree and calopo would perform better than the other species as cover crops in tree plantations, where they would be subjected to high levels of shading. However, management of the tree canopy would be important to allow sufficient light through to achieve acceptable growth rates in the cover crops.

Introduction

Soils under plantation crops, such as cacao (*Theobroma cacao*), have been degraded owing to wide space planting, loss of tree cover and long-term cultivation with no addition of fertiliser or lime. Soil degradation has occurred mainly through soil erosion, plant removal and leaching of nutrients. Growing of perennial legume cover crops as understory plants in cacao plantations would offer a number of benefits, including protection from soil erosion, weed suppression, improved soil quality and enrichment of soil by fixation of atmospheric nitrogen (Cunningham and Smith 1961; Wood and Lass 2001).

Survival and persistence of understory cover crops depend largely on the amount and quality of light reaching their canopies (Wilson and Ludlow 1991; Wong 1991; Wilson 1999). In tropical regions, the incoming photosynthetic active radiation (PAR) is around 1800 μmol/m²/s (Grace *et al.* 1998), but understory plants in rainforests, where tree density is very high, receive only 4–10% of this incoming PAR (Miyaji *et al.* 1997; Liang *et al.* 2001). Intermittently, understory plants also receive high levels of PAR in the form of sunflecks and through particular orientation of the sun (Tang *et al.* 1999). In the tropics, plantation crops are often established on newly cleared forest lands, where soil can be degraded through soil loss by erosion. Growing cover crops in the early stages of plantation establishment can reduce this soil loss. While cover crops receive

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full sunlight at this stage of plantation development, the incoming photosynthetic photon flux density (PPFD) is reduced as trees grow. In agroforestry-based plantation systems, canopies of shade trees and cacao together gradually reduce the incoming PPFD at the cover crop canopy level (Miyaji *et al.* 1997; Wilson 1999).

Shading reduces yields of most tropical legumes (Wong 1991; Fujita *et al.* 1993; Izaguirre-Mayoral *et al.* 1995), and it is vital to understand how cover crops respond to changing PPFD from full sunlight to dense shade. Cover crop species that tolerate lower PPFD have better chances of growing and persisting as understory plants in agroforestry-based cacao plantings. While inter-/intra-specific differences for shade tolerance in tropical cover crop/forage legumes have been reported (Wong *et al.* 1985; Shelton *et al.* 1987; Chong *et al.* 2001; Stur 2001), information concerning the effects of varying PPFD levels on net photosynthesis (Pn) in many of the tropical cover crop legumes is lacking.

The carbon dioxide concentration [CO₂] in the atmosphere has risen from 280 cm³/m³ in 1900 to present day levels of around 370 cm³/m³ and is expected to reach around 700 cm³/m³ by the end of the 21st century (Bolin 1998). In addition to this general global increase in [CO₂], increased litter decomposition in plantation crops contributes additional [CO₂] at ground level. Elevated atmospheric [CO₂] has contributed to increased plant biomass and net photosynthesis (Hogan *et al.* 1991; Amthor 1995; Long *et al.* 2004).

It has been projected that, owing to increases in trace gases including CO₂ in the atmosphere, global surface temperature is likely to increase by 5.8°C by the end of this century (Wilson and Mitchell 1987; Houghton *et al.* 2001). Ambient temperature has a profound effect on radiation use efficiency in legumes (Sinclair and Muchow 1999; Awal and Ikeda 2003). Reported studies on climatic changes, such as elevated [CO₂] and temperature, have focused primarily on temperate legume species (Cure and Acock 1986; Hogan *et al.* 1991; Amthor 1995; Long *et al.* 2004; Vu 2005). Little is known regarding the effects of increased [CO₂] and temperature and reduced light conditions on net photosynthesis of understory perennial tropical legumes.

The objective of our study was to develop an understanding of the effects of variation in environmental factors, such as PPFD, temperature and carbon dioxide concentrations [CO₂], on net

photosynthesis (Pn) and its components, such as stomatal conductance (Gs), transpiration (E) and internal CO₂ concentration (Ci), of perennial legume cover crop species for potential use as understory plants in cacao plantations.

Materials and methods

Cover crops and growth conditions

The 5 prominent cover crops selected for this study were: perennial peanut (*Arachis pintoi*), calopo (*Calopogonium mucunoides*), jack bean (*Canavalia ensiformis*), white lead tree (*Leucaena leucocephala*) and mucuna (*Mucuna pruriens*). Perennial peanut is a stoloniferous, perennial herb, native to South America, and can produce 5–10 t/ha/yr of dry matter (DM). It is somewhat tolerant of shade and can tolerate high levels of soil manganese and aluminium (Cook 1992). Calopo, a vigorous, twining perennial herb, native to tropical America, can produce 4–6 t/ha/yr of DM, can fix 250–450 kg/ha/yr of nitrogen, and is used mainly as a cover crop in tropical tree plantations (Chen and Aminah 1992). Jack bean is a climbing perennial herb, native from Mexico to Brazil. It is used as a cover crop, produces 1–6 t/ha/yr of DM and fixes 35–55 kg/ha/yr of N. It is tolerant of shade and drought (Duke 1981). White lead tree is a small perennial tree, native to the Yucatan Peninsula in Mexico. If used as a cover crop, it can produce 1–15 t/ha/yr of DM and fix 500 kg/ha/yr of N. It is very tolerant of shade and drought (Jones *et al.* 1992). Mucuna is a vigorous, twining herb, native to southern China, which is used as a cover crop and can produce 2–12 t/ha/yr of DM and fix 50–330 kg/ha/yr of N. It is easy to establish but lacks drought tolerance (Wulijarni-Soetjipto and Maligalig 1997). With the exception of perennial peanut, seeds of the cover crops were received from the Globo Rural Seed Company, Goiania, Go Brazil. Perennial peanut seeds (variety CIAT-17434) were received from Koolau Seed Supply Company, Kaneohe, HI.

Seeds of calopo, mucuna, jack bean and white lead tree were sown in 20-cm diameter plastic pots containing 2:2:1 sand:perlite:promix medium (pH 5.0). For each species, 3 pots were used. The growth medium was prepared by mixing sand, perlite and promix (Premier Horticulture Products, Quakertown, PA) in a cement mixer along

with required macro- and micronutrients to provide supplemental nutrients (mg/kg) of 600 N, 600 P, 240 K, 1012 Ca, 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 (The Scotts Company, Marysville, Ohio), triple superphosphate, urea, calcium sulphate, dolomitic lime and Scott's Micromix. Ten seeds of each legume species were planted in each pot and watered to adjust soil moisture levels to field capacity. Water was applied as needed on alternate days to maintain soil moisture at field capacity. Plants were grown for 36 days in a greenhouse under $400 \pm 50 \mu\text{mol}/\text{m}^2/\text{s}$ of PPFD, $450 \pm 50 \text{ cm}^3/\text{m}^3$ of carbon dioxide and a temperature of 30°C during the day and 24°C at night. On the 37th day of growth, plants were moved to a controlled environment chamber for photosynthetic measurements. Growth conditions in the growth chamber were: $400 \mu\text{mol}/\text{m}^2/\text{s}$ of PPFD for 12 h, $370 \pm 30 \text{ cm}^3/\text{m}^3$ of carbon dioxide concentration and a constant temperature of 25°C .

The sand:perlite:promix (2:2:1) mix alone was too dry for perennial peanut and the plants did not survive. Therefore, perennial peanut seeds were planted in the greenhouse in 4-cm diameter cell packs containing 100% promix (pH 6.0). Growth conditions were similar to those for the other legumes. After 55 days, seedlings were transplanted into 20-cm plastic pots containing 100% promix supplemented with 2.4 g/kg of Osmocote 18-6-12 and moved to glasshouses where the conditions were: $400 \pm 50 \mu\text{mol}/\text{m}^2/\text{s}$ of PPFD, $450 \pm 30 \text{ cm}^3/\text{m}^3$ of carbon dioxide and a temperature of 30°C during the day and 28°C at night. Plants were grown in these conditions for 24 days and watered as needed to maintain soil moisture at field capacity. The slow establishment and development of perennial peanut made it necessary to grow it under different conditions from the other legumes. On the 85th day of growth, perennial peanuts were moved into the growth chamber for photosynthetic measurements under growth conditions similar to those used for the other legumes.

Determination of net photosynthesis and its components (Ci, Gs, E)

After 2 days in the growth chamber, 3 plants per species were subjected to photosynthetic determinations. Photosynthesis was measured on the

third fully opened leaf from the top of each plant using a CIRAS-2 portable gas exchange system (PP Systems, Haverhill, Mass, USA) with a 2.5 cm^2 leaf chamber. The air flow rate was $200 \text{ cm}^3/\text{s}$. PPFD was supplied by the CIRAS LED light source. Temperature was controlled by peltier elements on the leaf chamber unit. $[\text{CO}_2]$ was controlled by the CIRAS-2 instrument. Standard deviation of data points of various measurements of each leaf were determined by SigmaPlot Ver. 10 and values were plotted on a graph.

Experiment I: Effects of light intensity

The effects of PPFD were determined on the cover crops with the CIRAS-2 system. A leaf was placed in the cuvette at a PPFD of $1500 \mu\text{mol}/\text{m}^2/\text{s}$, temperature of 30°C , carbon dioxide concentration of $400 \text{ cm}^3/\text{m}^3$ and vapour pressure deficit (VPD) 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 and $50 \mu\text{mol}/\text{m}^2/\text{s}$. Pn and its components (Ci, Gs, E) were recorded.

Experiment II: Effects of carbon dioxide concentration

The effects of carbon dioxide concentration $[\text{CO}_2]$ were determined on the cover crops using the CIRAS-2 system. A leaf was placed in the cuvette at $[\text{CO}_2]$ of $400 \text{ cm}^3/\text{m}^3$ with PPFD of $1500 \mu\text{mol}/\text{m}^2/\text{s}$, temperature of 30°C and VPD of 2.0–2.5 kPa. After the leaf gas exchange became constant, $[\text{CO}_2]$ was adjusted to 100, 250, 700 and $1000 \text{ cm}^3/\text{m}^3$. Pn and its components (Ci, Gs, E) were recorded.

Experiment III: Effects of temperature

The effects of temperature were determined on the cover crops with the CIRAS-2 system. A leaf was placed in the cuvette and the leaf temperature was adjusted to 25°C . The PPFD was maintained at $1500 \mu\text{mol}/\text{m}^2/\text{s}$ with the carbon dioxide concentration at $400 \text{ cm}^3/\text{m}^3$. The water vapour pressure of the air entering the leaf chamber was constant, and the VPD thus increased with measurement temperature. The average VPD across species was 2.0, 2.4, 2.8 and 4.3 kPa at 25, 28,

30 and 35°C, respectively. After the leaf gas exchange became constant, the leaf 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 Pn and its components (Ci, Gs, E) were recorded.

Results

Effects of PPFD

Overall, Pn values decreased as PPFD decreased from 1000 to 50 $\mu\text{mol}/\text{m}^2/\text{s}$, with a reduction of 90% in calopo, jack bean and white lead tree. Pn values in the various species were widely divergent at 1500 $\mu\text{mol}/\text{m}^2/\text{s}$ and converged as PPFD decreased, reaching similar levels at 100 $\mu\text{mol}/\text{m}^2/\text{s}$ PPFD. While Pn in mucuna, jack bean and perennial peanut seemed to reach a maximum at PPFD of 500 $\mu\text{mol}/\text{m}^2/\text{s}$ (Figure 1A), Pn of white lead tree was still increasing at 1500 $\mu\text{mol}/\text{m}^2/\text{s}$,

suggesting that this species would respond to higher levels of PPFD. In general, at high PPFD, mucuna recorded the lowest Pn of all legume species tested, while white lead tree recorded the highest values.

Internal CO_2 (Ci) increased as the PPFD decreased for all legume species (Figure 1B) with jack bean apparently the most sensitive and mucuna the least sensitive. The increasing Ci with decreasing PPFD was inversely related to the decrease in Pn.

With the exception of perennial peanut, stomatal conductance (Gs) in these legume species decreased with decreasing PPFD from 1000 $\mu\text{mol}/\text{m}^2/\text{s}$ (Figure 1C). Increases in PPFD from 1000 to 1500 $\mu\text{mol}/\text{m}^2/\text{s}$ slightly decreased Gs in perennial peanut, calopo and mucuna, suggesting that higher irradiance was inhibitory. Transpiration (E) followed patterns similar to those of Gs (Figure 1D).

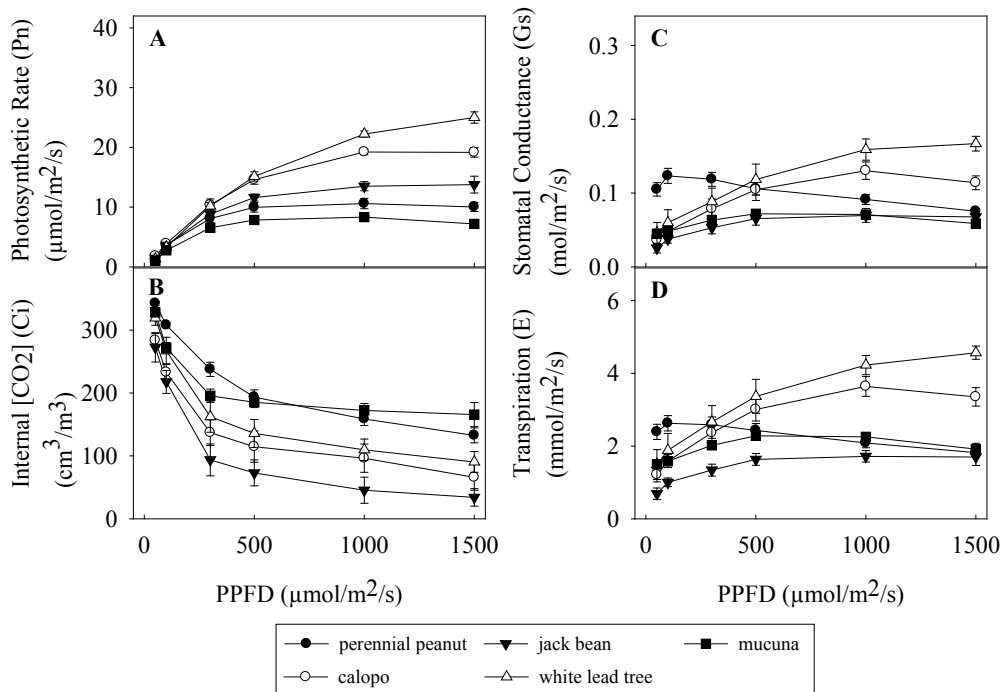


Figure 1. Effects of PPFD levels on: (A) net photosynthetic rate, Pn; (B) internal CO_2 concentration, Ci; (C) stomatal conductance, Gs; and (D) transpiration rate, E of 5 cover crop species at 30°C and 400 cm^3/m^3 of CO_2 . Each symbol represents the average of 3 replicates.

Effects of [CO₂]

Increasing the external [CO₂] increased Pn in all species (Figure 2A). Overall, increasing [CO₂] from 100 to 700 cm³/m³ increased the Pn 6-fold, with further increases in [CO₂] to 1000 cm³/m³ enlarging the overall response to 7-fold.

Inter-specific differences in Pn were noted at varying external [CO₂] levels. *Mucuna* showed the lowest and white lead tree the highest Pn values at all [CO₂] levels, with calopo and jack bean being intermediate. In all species except jack bean, Ci increased as external [CO₂] increased (Figure 2B).

Increases in [CO₂] affected Gs of the different species differently (Figure 2C). While Gs in white lead tree was halved by increasing [CO₂] from 100 to 1000 cm³/m³, much smaller reductions occurred in *mucuna* and jack bean and there was no change in perennial peanut and calopo. Transpiration (E) followed patterns similar to those of Gs (Figure 2D).

Effects of temperature

Overall, responses to changes in ambient temperature were much smaller than those to changes in PPFD and [CO₂]. Increasing the ambient temperature from 25°C to 30°C increased Pn in all species, and a further increase to 35°C produced a non-significant decrease in Pn in calopo, jack bean and *mucuna* (Figure 3A). Increasing the temperature from 30°C to 35°C increased Pn only slightly in white lead tree and perennial peanut. At all temperatures, white lead tree showed the highest Pn and perennial peanut the lowest. *Mucuna* reached its highest Pn at 28°C, calopo and jack bean at 30°C.

In general, in all species, Ci decreased as the external temperature increased, and was inversely related to the increase in Pn (Figure 3B).

Gs at any given external temperature varied with the plant species (Figure 3C), being higher for white lead tree and calopo than for the remaining species. For *mucuna*, Gs increased with

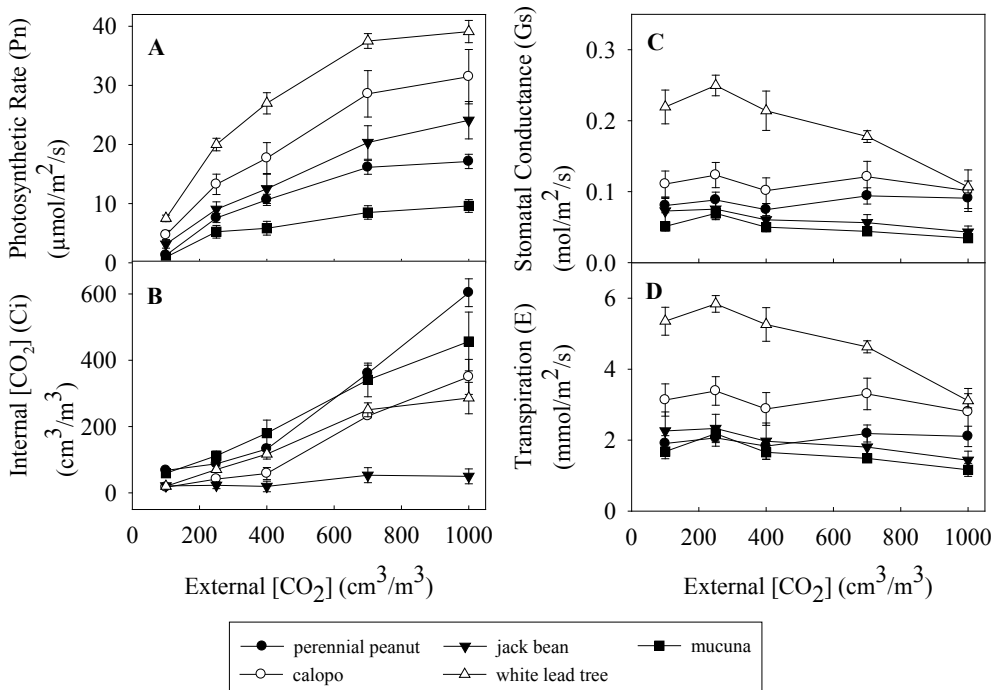


Figure 2. Effects of external CO₂ levels on: (A) net photosynthetic rate, Pn; (B) internal CO₂ concentration, Ci; (C) stomatal conductance, Gs; and (D) transpiration rate, E of 5 cover crop species at 30°C and 1500 μmol/m²/s PPFD. Each symbol represents the average of 3 replicates.

increasing leaf temperature up to 28°C, and then decreased with further increases in external temperature. Gs of calopo and jack bean increased up to 30°C, and then decreased, while that of white lead tree remained relatively constant and Gs of perennial peanut increased slightly as the temperature increased within the range of 25°C to 35°C. Transpiration (E) generally increased with temperature (Figure 3D), with higher values in white lead tree and calopo than in the remaining species

Discussion

This study has shown how sensitive these forage legumes are to changes in both incident radiation and atmospheric CO₂ levels. The legumes used here were very sensitive to low irradiance, confirming the conclusions of Ludlow and Wilson (1971) and Wilson and Ludlow (1991) that net photosynthesis of understory legumes is influenced by the amount of PPFD reaching the cover

crop canopy. None of the legumes grew well at low PPFD levels.

Soils receive nearly full sunlight early in cacao establishment, but the amount of light that reaches the soil is reduced as the trees grow. Miyaji *et al.* (1997) reported that, in well established shaded and non-shaded cacao plantations of Bahia Brazil at noon, light intensity above the cacao canopy fluctuated between 600 and 2000 μmol/m²/s (full sunlight). However, at ground level, the light intensity was as low as 4–10% (80–200 μmol/m²/s) of full sunlight. Our findings indicate that all species tested would photosynthesise and grow adequately in newly established plantations (full sunlight), with white lead tree and calopo producing highest yields. However, growth would be reduced dramatically as the trees matured and incident light levels fell below 300–500 μmol/m²/s, with much smaller differences in yields between species. This confirms anecdotal evidence that cover crops do well soon after cacao planting due to high light

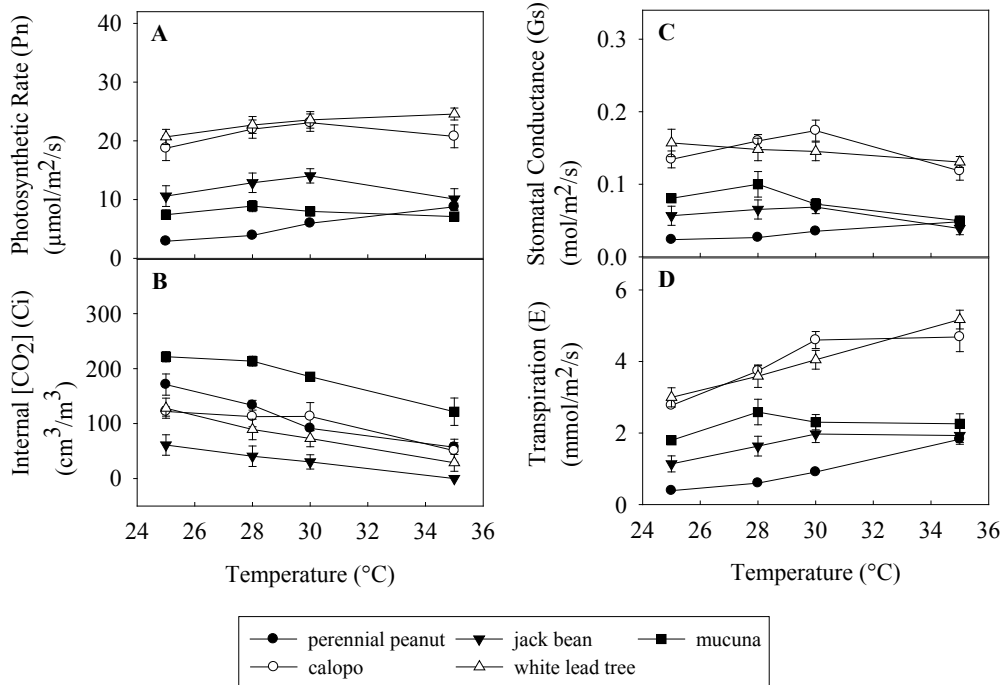


Figure 3. Effects of temperature on: (A) net photosynthetic rate, Pn; (B) internal CO₂ concentration, Ci; (C) stomatal conductance, Gs; and (D) transpiration rate, E of 5 cover crop species at PPFD of 1500 μmol/m²/s and 400 cm³/m³ of CO₂. Each symbol represents the average of 3 replicates.

availability, reducing soil loss by erosion and improving soil fertility by fixing N and adding organic residues. However, in older plantations, growth, persistence and effectiveness of cover crops are reduced owing to low light intensity.

In the legume species studied here, Pn at lower PPFD levels was lower than reported in the literature for temperate and tropical legumes; however, Pn at higher PPFD levels was comparable with those reported for temperate and tropical legumes (Wilson and Ludlow 1991; Bunce 1993). The differential responses to shading among species support earlier reports of inter-/intra-specific differences in shade tolerance of tropical legumes (Eriksen and Whitney 1982; Wong *et al.* 1985; Shelton *et al.* 1987; Baligar *et al.* 2006, 2008). While jack bean and white lead tree are known to tolerate shade effectively under tropical plantation systems (Duke 1981; Jones *et al.* 1992), white lead tree produced much more growth than jack bean at high levels of incident light. Perennial peanut is also considered somewhat tolerant of shade (Cook 1992), and Chen and Aminah (1992) reported that calopo was used as a cover crop in tropical tree plantations. The higher Pn of white lead tree and calopo at low PPFD in the current study supports the earlier findings, although yield differences between species were much lower than at high light levels. Cover crops that tolerate lower PPFD have a better chance of growing as understory plants and protecting soil longer in plantation crops. Therefore, management of cacao and shade tree canopies is critical to keeping these legumes productive. High PPFD received through sunflecks and orientation of the sun over the plantation might help to improve Pn of understory plants that are less tolerant of high levels of shade and will respond to high levels of incident light. In understory plants of evergreen forests, stomatal conductance is an important factor affecting the photosynthetic response to sunflecks (Kirschbaum and Pearcy 1988; Hogan *et al.* 1991). Increasing stomatal conductance with increasing PPFD is necessary to support higher Pn. It was significant in our study that all species which produced high Pn levels also displayed high stomatal conductance. However, high stomatal conductance owing to wide stomatal openings increases water loss through high evapotranspiration, which can be detrimental by inducing water stress in low rainfall situations.

Our findings confirm the earlier findings of Kimball (1983) and Drake and Leadley (1991)

that high atmospheric [CO₂] generally leads to increased Pn rates in C₃ plant species and decreases in stomatal conductance and transpiration. The photosynthetic responses observed in this study suggest that increasing atmospheric [CO₂] will have beneficial effects on Pn of these perennial legumes, especially white lead tree. If the predicted global atmospheric CO₂ concentrations of around 700 cm³/m³ by the end of the 21st century are realised (Bolin 1998), these forage species would respond well to the new conditions in tropical plantations. Bhagsari and Brown (1976) have reported inter-specific differences in photosynthetic rate to varying [CO₂] levels as found in our study. In peanut (*Arachis hypogaea*), increasing external [CO₂] from 400 to 800 cm³/m³ increased Pn but further increases in [CO₂] to 1200 cm³/m³ reduced Pn (Stancel *et al.* 2000). Similarly, Vu (2005) reported that leaves of peanut (*Arachis hypogaea*) plants grown under elevated [CO₂] (720 cm³/m³) had higher Pn values than plants grown under ambient [CO₂] (360 cm³/m³). Higher [CO₂] might also allow understory plants to exploit sunflecks more efficiently. This is important as sunflecks can account for 40% or more of the total daily photon flux density received by the understory plants in evergreen forests (Pearcy 1983; Chazdon and Fetcher 1984).

Elevated CO₂ is known to decrease evapotranspiration through reduction of Gs in most plants (Morison 1998; Long *et al.* 2004). Doubling of atmospheric CO₂ levels can reduce Gs in C₃ annual plants by an average of 34% (Cure and Acock 1986). However, over a comparable range of CO₂ levels in this study, only white lead tree had a significant reduction in Gs or E.

It was interesting that temperature changes of the magnitude tested in this study had the least effect on responses of cover crops, since Sinclair and Muchow (1999) and Awal and Ikeda (2003) indicated that ambient temperature had a profound effect on radiation use efficiency in legumes. This suggests that shading and elevation of [CO₂] would have much greater effects on growth of these forages than the projected increases in global surface temperature of 5.8°C by the end of this century (Wilson and Mitchell 1987; Houghton *et al.* 2001). As shade from trees mitigates warming of the soil and air above the canopy of understory plants (Chen 1989; Wilson and Ludlow 1991), **any increase in global temperature would be reduced in plantations.** While

temperature optima for many tropical legumes have been reported in the range of 15–35°C (Cooper 1973; Duke 2002; Cook *et al.* 2005), we were unable to locate in the literature values for the optimal temperatures required for achieving maximum Pn in the legumes used in our study. The small reduction in Pn at the highest temperature recorded in this study could be due to the deactivation of the Rubisco enzyme which controls photosynthesis (Crafts-Brandner and Salvucci 2000). The slight decreases in Pn in mucuna, calopo and jack bean above 30°C suggest that these species may be better adapted to cooler understory conditions.

Conclusions

Tropical legume cover crops are important components in cropping systems to improve soil fertility and reduce soil degradation. Results obtained in our study show large variations in photosynthesis or growth of 5 legume cover crops in response to changes in solar radiation, temperature and carbon dioxide concentration. Shade management of the overstory trees is critical in maintaining productivity of these tropical perennial legumes in tree plantations. White lead tree and calopo had the highest photosynthetic rates and mucuna had the lowest rate at low levels of solar radiation, high carbon dioxide concentration and moderate temperatures, conditions which should exist under established tree plantations. In addition, these species performed much better than the remaining species at high levels of incident light, as would prevail during the early stages of establishment of the tree plantation. This suggests that white lead tree and calopo show most promise for growing under these conditions. There is need for evaluation of inter-/intra-specific differences in performance of legume cover crops under different perennial cropping systems of South America, in order to identify suitable legume cover crops that offer maximum benefits to various agro-ecological regions.

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