

Chapter 5

Light Intensity Effects on Growth and Nutrient-use Efficiency of Tropical Legume Cover Crops

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Introduction

In the tropics, plantation crops are established on newly cleared forest lands with a wide spacing between rows and within rows. For example, cacao (*Theobroma cacao*) on newly cleared forest lands is being planted with wide spacing of 1.2×1.2 m to 5.0×5.0 m (Wilson, 1999). Under such a planting pattern, the soil is unprotected during early plantation growth, and is subject to erosion and nutrient leaching. Planting a fast-growing cover crop in early stages of plantation crop establishment might help to reduce soil erosion and increase soil organic matter content, leading to restoration of soil fertility and productivity (Cunningham and Smith, 1961; Wood and Lass, 2001). In addition, cover crops are known to improve soil water-holding capacity, increase biological activities, suppress weed growth, and decrease effects of diseases and insects (Maesen and Somaatmadja, 1989; Blevins and Frye, 1993; Wessel and Maesen, 1997; Teasdale, 1998).

In cacao plantations, legume cover crops fix N and provide shade to early growing cacao and minimize the loss of soil by erosion (Wood and Lass, 2001). Beneficial effects of limited number of cover crops in improving growth and yield of cacao have been reported (Jordan and Opoku, 1966; Opoku, 1970; Wilson, 1999). Species such as *Calapogonium muconoides*, *Crotalaria striata*, *Flemingia macrophylla*, *Pueraria javanica*, *P. phaseoloides*, *Sesbania punctata*, *Tephrosia candida*, and *Tephrosia vogelii* have been used as cover crops (Wilson, 1999; Wood and Lass, 2001). Limited numbers of other valuable legume cover crops have been evaluated for their compatibility with cacao. Many legume cover crops such as joint vetch

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(*Aeschynomene americana*), sunhemp/Indian hemp (*Crotalaria juncea* L.), crotalaria ochroleuca (*Crotolari ochroleuca*), showy crotalaria/crotalaria spectabilis (*Crotalaria spectabilis*), hairy indigo (*Indigofera hirsute* L), lab-lab (*Lablab purpureus*), sesbania (*Sesbania microcarpa*), Brazilian lucern/Brazilian stylo (*Stylosanthes guianensis*), and cow pea/Fejao caupi (*Vigna unguiculata*) are tolerant to high, prevailing tropical temperatures, and rainfall conditions, and adaptable to wide range of pH's that are common in the tropical soils (Duke, 1981; Wessel and Maesen, 1997). However, information is lacking of their suitability as cover crops and ability to grow in low light intensities in plantation crops such as cacao.

Solar radiation intensity and interception by plants are fundamental processes governing crop growth and yield. A close relationship between light interception and yield has been demonstrated for a large variety of plant species (Monteith, 1977). In tropical regions, incoming photosynthetically active radiation is around $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Grace et al. 1998). Plantation crops, such as cacao, are sensitive to high light intensity and are therefore grown under various types of shade trees (Wood and Lass, 2001). For young cacao about 50% shade is optimum and amount of radiation observed at canopy level has been $800\text{--}900 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Wood and Lass, 2001). When cover crops are grown under plantation crops, growth of cover crops is influenced by the amount of photosynthetic photon flux density (PPFD) reaching the cover crop (Wilson, 1999). Canopies of shade trees and cacao together reduce the amount of PPFD at the cover crop canopy levels. In tropical forest depending on the leaf canopy density, understory plants receive around 2% of the PPFD that is received at the upper canopy levels, and understory crops also receive intermittently high levels of PPFD in sunflecks (Liang et al. 2001). Cover crop species that tolerate lower PPFD protect the soil longer in plantation crops and improve its fertility.

The legume cover crops chosen for this study have great potentials as suitable cover crops for cacao plantation, mainly because they sustain many of the prevailing abiotic stresses that are common in the tropical plantation crops. However, their ability to grow at low light intensity is unknown. The objective of our study was to evaluate the influence of low levels of PPFD on growth and nutrient uptake and use efficiency of nine tropical legume cover crops.

Materials and Methods

A growth chamber experiment was conducted at Beltsville Agricultural Research Center, Beltsville, Maryland, with a day temperature of 30°C at 65% relative humidity, and a night temperature of 28°C at 65% relative humidity. In South America, cacao is grown under such climatic conditions (Wood and Lass, 2001) and therefore we selected these temperature and humidity values to test the cover crops, mainly because these crops will be grown as an understory plants in cacao plantation. Plants were subjected to 14h of light and 10h of darkness daily. Plants were grown at two photosynthetic photon flux densities (PPFD) as light treatments: $200 \mu\text{mole m}^{-2} \text{s}^{-1}$ and $400 \mu\text{mole m}^{-2} \text{s}^{-1}$. These selected light treatments represent about 10–20% of

the PPFD received in the tropical region. Within the growth room, mini chambers were constructed with 2 cm diameter PVC pipe and covered with various layers of plastic shade cloth to achieve desired PPFD.

Nine annual erect shrub-type leguminous cover crops were used in this study (Table 5.1). These include: Joint Vetch (*Aeschynomene americana*), Sunhemp/Indian hemp (*Crotalaria juncea* L.), *Crotalaria ochroleuca* (*Crotalaria ochroleuca*), Showy crotalaria/*Crotalaria spectabilis* (*Crotalaria spectabilis*), Hairy indigo (*Indigofera hirsute* L), Lab-lab (*Lablab purpureus*), Sesbania (*Sesbania microcarpa*), Brazilian lucern/Brazilian stylo (*Stylosanthes guianensis*), and Cow pea/Fejao caupi (*Vigna unguiculata*). Twenty seeds of each legume cover crop were planted in black plastic pots containing 2 kg of perlite/sand/ promix (2:2:1 volume basis) with adequate bottom drainage. Osmocoat (18-6-12, Scotts, Marysville, OH), triple super phosphate, urea, CaSO₄, dolomitic lime, and Scotts micromax were mixed with growth medium to provide 600N, 600P, 240K, 1012Ca, 309Mg, 500S, 119Fe, 0.7B, 17.5Mn, 7.0Cu, 7.0Zn, and 0.35Mo mg kg⁻¹. Every other day pots were weighed and desired amount of deionized water was added to maintain growth medium water level at field capacity. Amount of water held at field capacity was determined by placing saturated potting mixture in cylinder and allowing it to drain for 48h and moisture content was determined by drying soil at 110°C until constant weight is reached. Amount of water held by the growth mixture was considered as field capacity moisture content.

On the 10th day of growth, plants in each pot were thinned to keep two plants per pot for larger growing species and seven plants per pot for smaller growing species. Seedlings that were removed with root intact were used for determination of initial growth (shoot dry weight, leaf area, stem height, root length, and root dry weight) and nutrient uptake parameters were recorded (baseline harvest). After 45 days of growth all remaining plants were harvested, and roots and shoots were separated and washed with deionized water. Leaves were separated from stem and leaf area was determined with Li-Cor model 300 leaf area meter (Li-Cor Inc., Lincoln, NB) and stem height was recorded. Root and shoots were dried at 70°C for 5 days and dry weight was recorded. Shoot samples were ground to pass a 0.55 mm mesh sieve. Chemical analysis of the shoot samples was done at the A&L Southern Agricultural Lab, Pompano Beach, FL, by adapting modified methods suggested by Wolf (1982). Plant samples were wet digested in concentrated sulfuric acid and 30% hydrogen peroxide. Gilford STASAR II spectrophotometer was used to determine N and P, and Perkin Elmer Analyst 400 Atomic Absorption Spectrophotometer was used to determine the K, Ca, Mg, and Na. Plant samples were wet digested in muffle furnace at 600°C with magnesium nitrate and dissolved in 1:1 HCl, and S concentration was determined by colorimetric method by use of Gilford STASAR II spectrophotometer.

The following growth and nutrient uptake parameters were determined.

Specific leaf area (SLA, cm²/g) = [Total leaf area, cm²/Total leaf dry wt, g]

Leaf area ratio (LAR, cm²/g) = [Total leaf area, cm²/Shoot + Root dry wt, g]

Leaf mass/Unit leaf area (LMA, g/cm²) = [1/SLA]

Root/Shoot ratio(R/S) = [Wr/Ws], where Wr is root weight and Ws is shoot weight

Table 5.1 Shoot, root, and leaf growth parameters, RGR and NAR of leguminous cover crops as influenced by varying PPFD^a

| Species | PPFD ^b | Shoot wt g/plant | Root wt g/plant | R/S | RGR ×10 ² | NAR ×10 ⁴ | LA cm ² /plant | SLA cm ² /g | LAR cm ² /g | LMA g/cm ² |
|------------------|-------------------|---------------------|--------------------|---------|-------------------------|-------------------------|------------------------------|---------------------------|---------------------------|--------------------------|
| Joint Vetch | L ₁ | 0.67f-h | 0.06b | 0.08a-c | 15b | 10.4d | 105.68f | 250.48ef | 147.16f-h | 4.0cd |
| | L ₂ | 1.33e-g | 0.15b | 0.11a-c | 16b | 16.1c | 149.38ef | 175.74g | 100.53hi | 5.7b |
| Sunhemp | L ₁ | 1.39d-f | 0.10b | 0.07a-c | 10d | 4.5gh | 338.52de | 406.61b | 241.63bc | 2.5f-h |
| | L ₂ | 4.62a | 0.47a | 0.10a-c | 13c | 9.1de | 762.07b | 309.52de | 148.82e-h | 3.3e-g |
| Crotoloria ochro | L ₁ | 0.56gh | 0.04b | 0.08a-c | 14c | 6.9e-g | 119.45ef | 338.14cd | 199.57b-e | 3.0d-g |
| | L ₂ | 1.37d-f | 0.15b | 0.11a-c | 15b | 10.9d | 209.11ef | 266.26ef | 141.24gh | 3.9c-e |
| Showy crotolaria | L ₁ | 0.79e-f | 0.12b | 0.16a | 13c | 5.2gh | 225.92ef | 396.78bc | 245.93bc | 2.5f-h |
| | L ₂ | 1.68d | 0.24ab | 0.14ab | 13c | 5.4f-h | 484.27cd | 405.71b | 251.15d | 2.5gh |
| Hairy indigo | L ₁ | 0.54h | 0.02b | 0.03c | 15b | 8.7d-f | 97.93f | 287.54d-f | 176.07d-g | 3.5e-f |
| | L ₂ | 1.48de | 0.08b | 0.06bc | 17a | 11.9d | 227.35ef | 243.53f | 148.31e-h | 4.1c |
| Lab-lab | L ₁ | 3.31bc | 0.48a | 0.15ab | 10de | 3.0h | 1223.62a | 587.36a | 324.45a | 1.7h |
| | L ₂ | 3.17c | 0.14b | 0.05c | 10de | 3.0h | 1134.15a | 599.21a | 337.88a | 1.7h |
| Sesbania | L ₁ | 1.90d | 0.21ab | 0.11a-c | 16b | 24.1b | 133.46ef | 134.46g | 68.10i | 7.8a |
| | L ₂ | 3.94a-c | 0.46a | 0.12a-c | 18a | 35.6a | 224.03ef | 123.12g | 50.90i | 8.1a |
| Brazilian stylo | L ₁ | 0.09h | 0.01b | 0.05c | 11d | 5.9e-h | 18.06f | 349.16b-d | 197.51c-f | 2.9e-g |
| | L ₂ | 0.28h | 0.01b | 0.05c | 13c | 6.6e-g | 58.75f | 306.19de | 203.86b-d | 3.3c-g |
| Cowpea | L ₁ | 3.47bc | 0.11b | 0.03c | 9e | 4.9gh | 654.93bc | 397.05bc | 181.73d-g | 2.5f-h |
| | L ₂ | 4.08ab | 0.15b | 0.04c | 9e | 6.6e-g | 577.95bc | 398.13bc | 135.62 | 2.5f-g |
| Mean | L ₁ | 1.41 | 0.13 | 0.08 | 13 | 8.2 | 324.17 | 349.73 | 198.02 | 3.4 |
| | L ₂ | 2.44 | 0.21 | 0.09 | 14 | 11.7 | 425.23 | 314.16 | 168.70 | 3.9 |
| Significance | | | | | | | | | | |
| Species (S) | | ** | * | * | ** | ** | ** | ** | ** | ** |
| PPFD (P) | | ** | NS | NS | ** | ** | * | ** | ** | ** |
| S × P | | ** | NS | NS | ** | ** | NS | NS | NS | NS |

Values within a column followed by the same letter are not significantly different ($P < 0.05$, Tukey's test).

** Significant at 0.05 and 0.01 levels of probability, respectively.

^aRGR = Relative growth rate, g/g/d; NAR = Net assimilation rate, g/cm²/d; R/S = Root/Shoot ratio; LA = Leaf area; SLA = Specific leaf area; LMA = [Leaf mass/Unit leaf area].

^bL₁ = PPFD (Photosynthetic photon flux density) of 200 μmol m⁻² s⁻¹; L₂ = PPFD of 400 μmol m⁻² s⁻¹.

Relative Growth Rate (RGR) = $[\ln (Wt_2/Wt_1)/(T_2-T_1)]$, where Wt is total weight (shoots + root), T is time interval in days, and 1 and 2 refers to initial and final harvest

Net assimilation rate (NAR) = $[RGR/LAR]$

Nutrient influx (IN) = $[(U_2-U_1)/(T_2-T_1)] \times [(\ln W_{r_2}-\ln W_{r_1})/(W_{r_2}-W_{r_1})]$, where U refers to elemental content of shoot ($\mu\text{mol}/\text{plant}$) and T is time in seconds, subscripts 1 and 2 refer to initial and final harvest time

Nutrient transport (TR) = $[(U_2-U_1)/(T_2-T_1)] \times [(\ln W_{s_2}-\ln W_{s_1})/(W_{s_2}-W_{s_1})]$

Nutrient use efficiency ratio (ER) = $[\text{mg of } W_s/\text{mg of any given element in shoot}]$

Treatments were replicated three times and data were subjected to analysis of variance using general linear model (GLM) procedures of SAS (Ver. 8, SAS Institute, Cary, NC).

Results and Discussion

Root and Shoot Growth

At both PPF levels significant variation was observed in growth parameters among different plant species (Table 5.1). Variation in shoot weight was $0.09\text{--}3.31 \text{ g plant}^{-1}$ at low PPF and $0.28\text{--}4.62 \text{ g plant}^{-1}$ at high PPF. When averaged across plant species, shoot weight was $1.41 \text{ g plant}^{-1}$ at low light intensity and $2.44 \text{ g plant}^{-1}$ at high light intensity. Overall increase in shoot dry weight was 73% at higher light intensity compared to lower light intensity. Similarly, overall increase in root dry weight was 62% at higher light intensity compared with lower light intensity. This indicates that shoot dry weight was more sensitive to light intensity than root weight. Overall, root weight was significantly correlated with shoot weight ($r=0.56$, $P<0.01$) indicating, a mutually beneficial effects of increasing light intensity on roots and shoots on each other.

Cowpea, sesbania, lab-lab, and sunhemp produced higher shoot and root dry weights at 200 and $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ of PPF compared to other species. Brazilian stylo and hairy indigo produced lowest shoot and root weight at both the PPF. The difference in growth and development among different plant species is associated with their complex genetic, physiological, and morphological determinants, which include photosynthesis, respiration, and water and mineral uptake (Krizek et al. 1985). Leaf area was also significantly correlated with root dry weight ($r=0.44$, $P<0.001$) and shoot weight ($r=0.72$, $P<0.01$).

Improvement in most of the growth parameters at higher light intensity was associated with enhanced photosynthesis, which leads to increased dry matter accumulations (Fageria, 1992; Fageria et al. 1997). Schittenhelm et al. (2004) reported that the economic yield of any crop is a function of the amount of light energy absorbed by the green foliage, the efficiency of the foliage to use the energy captured for biomass production, and the partitioning of the crop biomass to the

harvested plant part. Similarly, Whitman et al. (1985) reported that dry matter yield of crops increases in a quadratic fashion with increasing intercepted radiation.

For all legumes evaluated, plant species \times PPFD interactions were significant for shoot dry weight, relative growth rate (RGR) and net assimilation rate (NAR, a measure of the efficiency of plant leaves to produce dry matter), indicating that these plant growth parameters can be manipulated with the variation of PPFD intensities in favor of higher yield (Table 5.1). The overall improvement in relative growth rate was 8% at 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PPFD compared with 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PPFD (Table 5.1). Similarly, increase in net assimilation rate was 43% with the PPFD of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ compared to 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PPFD. Data in Table 5.1 show that among nine crop species, sesbania had the highest NAR at low as well as at high PPFD and lab-lab had lowest NAR values at both PPFD levels. The lower NAR rate of lab-lab may be due to its self shading of leaves and reduced photosynthetic efficiency of older leaves.

Nutrient Uptake and Use Efficiency

Uptake of all the macronutrients was significantly influenced by species, PPFD and species \times PPFD interactions (Table 5.2). Variations in nutrients uptake were related to differences in dry matter accumulation between species. For example, Brazilian stylo produced lowest dry matter yield and had the lowest nutrient uptake. Similarly, sunhemp and cowpea produced higher dry matter yields and accumulated higher nutrient levels. Nutrient uptake was significantly correlated with shoot dry weight. The correlation values were: N (0.99, $P < 0.01$), P (0.99, $P < 0.01$), K (0.97, $P < 0.01$), Ca (0.91, $P < 0.01$), Mg (0.91, $P < 0.01$), S (0.88, $P < 0.01$) and Na (0.65, $P < 0.01$). Such relationship clearly shows the significance of shoot demand on nutrient uptake.

Differences in nutrient uptake and yield among species have been related to differences in absorption, translocation, shoot demand, and dry matter production potentials per unit of nutrient absorbed (Baligar et al. 2001; Gerloff and Gabelman, 1983; Vose, 1984). Averaged across nine crop species, uptake of all the macronutrients was higher at higher PPFD. Furthermore, across crop species and light intensity, uptake of nutrient was in the order of $\text{N} > \text{K} > \text{Ca} > \text{P} > \text{S} > \text{Mg} > \text{Na}$. Fageria et al. (1997) reported similar trends in macronutrient uptake by legume crops. Most of the soluble N in well-drained cultivated soils is present in the nitrate form. These results also suggest that at high PPFD legume cover crops have high N requirement, therefore use of cover crops could lower the buildup of N in soil thereby reduce its leaching. Crop residue from these crops could also supply substantial amount of N to succeeding or companion plantation crops.

Nutrient efficiency ratio (mg shoot weight produced/mg nutrient accumulated in the shoot) of all the macronutrients was significantly influenced by crop species (Table 5.3). However, PPFD had a significant influence only for nutrient efficiency ratios of N, Na, K, and Mg. Crop species \times PPFD interaction was significant for all

Table 5.2 Influence of PPFD on uptake of macronutrients in different species of leguminous cover crops

| Species | PPFD ^a | N | P | S | Na mg plant ⁻¹ | K | Ca | Mg |
|------------------|-------------------|-----------|----------|----------|------------------------------|----------|----------|---------|
| Joint Vetch | L ₁ | 29.81fg | 8.83d-g | 4.39g-i | 0.25ef | 19.13d-g | 10.45e-h | 2.72f-h |
| | L ₂ | 58.09d-f | 15.12d | 7.47e-i | 0.18f | 34.49d-f | 19.03d-f | 5.61d-f |
| Sunhemp | L ₁ | 84.12de | 16.02d | 15.37c-e | 3.00bc | 41.54c-e | 21.40de | 5.14d-g |
| | L ₂ | 219.89a | 19.45a | 38.75a | 11.34a | 11.60ab | 68.26a | 20.80a |
| Crotalaria ochro | L ₁ | 33.48fg | 6.14e-g | 6.04f-i | 0.81d-f | 17.49d-g | 7.42f-h | 2.08gh |
| | L ₂ | 64.51d-f | 15.37d | 12.60c-g | 1.51c-f | 37.02de | 20.10d-f | 6.49de |
| Showy crotalaria | L ₁ | 44.05e-g | 6.07e-g | 8.42d-i | 0.56ef | 21.13d-g | 15.15e-h | 2.47f-h |
| | L ₂ | 94.67d | 13.55de | 16.46cd | 1.05d-f | 43.78cd | 32.32cd | 5.40d-g |
| Hairy indigo | L ₁ | 22.89fg | 3.23fg | 2.79hi | 0.13f | 16.56fg | 11.28e-h | 1.93gh |
| | L ₂ | 65.58d-f | 10.77d-f | 13.85c-f | 0.50ef | 41.37de | 35.27c | 6.74de |
| Lab-lab | L ₁ | 155.93bc | 35.12c | 19.60bc | 0.47ef | 115.34ab | 15.30ab | 8.47cd |
| | L ₂ | 140.03c | 35.37c | 11.13d-g | 0.32ef | 104.58b | 41.13c | 6.85de |
| Sesbania | L ₁ | 93.02d | 15.48d | 8.97d-h | 0.93d-f | 68.04c | 16.40e-g | 4.69e-g |
| | L ₂ | 197.78ab | 39.10bc | 20.60bc | 2.54cd | 117.24ab | 37.50c | 11.22c |
| Brazilian stylo | L ₁ | 3.50g | 0.80g | 0.56i | 0.06f | 2.72g | 1.43h | 0.21h |
| | L ₂ | 10.31g | 2.06g | 1.40hi | 0.06f | 7.89fg | 4.50gh | 0.63h |
| Cowpea | L ₁ | 160.15bc | 36.98c | 24.81b | 1.99c-e | 138.39a | 44.59bc | 16.95b |
| | L ₂ | 181.58a-c | 45.53ab | 25.55b | 4.36b | 124.22ab | 40.41c | 18.60ab |
| Mean | L ₁ | 69.66 | 14.30 | 10.11 | 0.91 | 48.93 | 15.94 | 4.96 |
| | L ₂ | 114.72 | 25.15 | 16.42 | 2.43 | 58.02 | 33.17 | 9.15 |
| Significance | | | | | | | | |
| Species (S) | | ** | ** | ** | ** | ** | ** | ** |
| PPFD (P) | | ** | ** | ** | ** | ** | ** | ** |
| S × P | | ** | ** | ** | ** | ** | ** | ** |

Values within a column followed by the same letter are not significantly different ($P < 0.05$, Tukey's test).

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

^a L₁ = PPFD (Photosynthetic Photon Flux Density) of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$; L₂ = PPFD of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Table 5.3 Influence of PPF on nutrient efficiency ratio of macronutrients in different species of leguminous cover crops

| Species | mg shoot mg element in shoot ⁻¹ | | | | | | | |
|-------------------|--|---------|---------|----------|-----------|---------|---------|----------|
| | PPFD ^a | N | P | S | Na | K | Ca | Mg |
| Joint Vetch | L ₁ | 22.7b,c | 75.3f | 152.0d-g | 2777.8b | 34.9e-f | 64.4b-d | 246.5d-f |
| | L ₂ | 23.0b,c | 89.7de | 179.5b-d | 8333.3a | 38.8a,b | 70.5b | 238.5d-f |
| Sunhemp | L ₁ | 17.6e,f | 85.6ef | 102.5gh | 842.1d,e | 32.4e-g | 64.9b-d | 270.4e-e |
| | L ₂ | 21.3b-d | 93.5de | 120.2e-h | 427.7e | 40.7a | 68.0b,c | 222.3e,f |
| Crotoloria ochro. | L ₁ | 16.9f | 91.2de | 93.3h | 756.2e | 32.2f-h | 75.5b | 268.5c-e |
| | L ₂ | 21.5b-d | 89.4d-f | 107.6fh- | 970.7de | 36.9c,d | 67.6b,c | 210.1f |
| Showy crotalaria | L ₁ | 17.8e,f | 129.8bc | 93.4h | 1476.2c-e | 37.7a-c | 52.4c,d | 321.1b,c |
| | L ₂ | 17.7e,f | 124.0bc | 102.1g,h | 1944.4c-e | 38.3a-c | 52.0c-e | 311.2b,c |
| Hairy indigo | L ₁ | 23.7b | 168.2a | 218.9b | 4444.4b | 32.7e-g | 48.2d,e | 285.5c,d |
| | L ₂ | 22.6b,c | 136.4b | 108.8e-h | 3055.6bc | 36.0b-e | 42.0e | 219.1e,f |
| Lab-lab | L ₁ | 21.3b-d | 93.9de | 196.9b-d | 8333.3a | 28.7h-j | 61.8b-d | 411.2a |
| | L ₂ | 22.9b,c | 90.9de | 286.1a | 10000.0a | 30.3g-i | 77.5b | 463.1a |
| Sesbania | L ₁ | 20.9c,d | 132.2b | 214.0b,c | 2777.8b-d | 28.3i,j | 113.8a | 427.1a |
| | L ₂ | 20.0d,e | 100.7d | 195.3b-d | 1619.0c-e | 33.9d-g | 104.8a | 353.3b |
| Brazilian stylo | L ₁ | 26.5a | 116.3c | 163.9b-e | 1428.6c-e | 34.0e-f | 64.9b-d | 434.8a |
| | L ₂ | 26.8a | 135.9b | 198.9b-d | 4444.4b | 35.0e-f | 62.0b-d | 442.5a |
| Cowpea | L ₁ | 21.7b-d | 94.1d,e | 147.9d-h | 1809.5c-e | 25.1j | 79.6b | 210.4f |
| | L ₂ | 22.5b-d | 89.6d,e | 160.8c-f | 988.1d,e | 32.9e-g | 108.1a | 221.3e,f |
| Mean | L ₁ | 21.0 | 109.6 | 153.6 | 2738.4 | 31.8 | 69.5 | 330.6 |
| | L ₂ | 22.1 | 105.6 | 162.1 | 3531.5 | 35.9 | 69.2 | 297.9 |
| Significance | | | | | | | | |
| Species (S) | | ** | ** | ** | ** | ** | ** | ** |
| PPFD (P) | | * | NS | NS | * | ** | NS | * |
| S × P | | * | ** | ** | ** | * | NS | * |

Values within a column followed by the same letter are not significantly different ($P < 0.05$, Tukey's test).

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

^aL₁ = PPF (Photosynthetic Photon Flux Density) of 200 μmol m⁻² s⁻¹; L₂ = PPF of 400 μmol m⁻² s⁻¹.

the macronutrient efficiency ratios with the exception of Ca. Significant crop species \times PPFD interaction suggests that crop variation in macronutrient utilization depends on light intensity. Across plant species and PPFD levels, nutrient utilization efficiency ratios were in the order of Na > Mg > S > P > Ca > N. Hence, legume cover crops evaluated in this study require maximum amounts of N and minimum amounts of Na to produce equal amount of dry matter. Plants that have high ER values for essential nutrients might produce well when grown on infertile soil where supply of nutrients is limited. Interspecific variation in mineral uptake and utilization in various plant species is well documented (Baligar et al. 2001; Baligar and Fageria, 1997; Gerloff and Gabelman, 1983; Vose, 1984). Variations in nutrient utilization within and between plant species are known to be under genetic and physiological control but are modified by plant interactions with environmental variables (Baligar and Fageria, 1997; Baligar et al. 2001).

Nutrient Influx and Transport

Macronutrient influx into roots was significantly affected by crop species; however, PPFD had no effect on nutrient influx (Table 5.4). At both PPFD's, hairy indigo had maximum influx of macro nutrients, and showy crotalaria had the minimum influx of N, P, K, and Mg. Overall, nutrient influx in to the root was in the order of N > K > Ca > P > S > Mg > Na.

Transport of all the micronutrients was significantly affected by crop species (Table 5.4). Whereas, PPFD significantly affected the transport of P, Ca, and Mg only. Similarly, crop species \times PPFD interactions were significant for transport of P, S, Ca, and Mg. Root morphological parameters such as length, surface area, volume dry weight (Hackett, 1969; Baligar et al. 2001), and physiological conditions of plants are known to affect plant nutrient uptake, influx, and transport (Drew et al. 1969; Pitman, 1972). Differences in nutrient influx and transport among plant species have been related to differences in shoot demand per unit of nutrient absorbed (Gerloff and Gabelman, 1983; Vose, 1984; Baligar and Fageria, 1997).

Conclusions

Nine cover crop species tested in this experiment expressed significantly different growth parameters and nutrient uptake, influx, transport, and utilization efficiency at different PPFD's. Hence, it is possible to select cover crop species, which may be suitable for different plantation crops with varying amounts of shade in improving soil fertility and conserving soil and water resources. Maximum growth of root, shoot, relative growth rate, and net assimilation rate, uptake of N, P, S, Na, K, Ca, and Mg was achieved at PPFD of $400 \mu\text{mole m}^{-2} \text{s}^{-1}$. Nutrient utilization efficiency was in the order of Na > Mg > S > P > Ca > N. Nutrient uptake significantly correlated

Table 5.4 Influence of PPF₂ on influx of macronutrients in different species of leguminous cover crops

| Species | PPFD ^a | | N | P | S | Na | K | Ca | Mg |
|-------------------|-------------------|----------------|----------|--------|--------|--------|---------|--------|--------|
| | L ₁ | L ₂ | | | | | | | |
| Joint Vetch | L ₁ | L ₂ | 59.6b-d | 8.0a | 3.8b,c | 0.3e-g | 13.8d-f | 7.3b-d | 3.1c-e |
| | L ₁ | L ₂ | 49.5c,d | 5.8a-d | 2.8b,c | 0.1g | 10.5d-f | 5.7b-d | 2.8d,e |
| Sunhemp | L ₁ | L ₂ | 54.3c,d | 4.8a-d | 4.3bc | 1.1a,b | 10.2d-f | 4.9b-d | 2.0e |
| | L ₁ | L ₂ | 45.9c,d | 4.7a-d | 3.5b,c | 1.4a | 8.5e,f | 5.0b-d | 2.5d,e |
| Crotalaria ochro. | L ₁ | L ₂ | 74.6a-d | 6.2a-d | 6.0b | 1.1a-c | 14.0d-f | 5.9b-d | 2.7d,e |
| | L ₁ | L ₂ | 52.3c,d | 5.6a-d | 4.5b,c | 0.8b-d | 10.8d-f | 5.8b-d | 3.0c-e |
| Showy crotalaria | L ₁ | L ₂ | 40.2d | 2.5c,d | 3.4b,c | 0.3e-g | 7.1f | 4.9b-d | 1.3d |
| | L ₁ | L ₂ | 41.8c,d | 2.7c,d | 3.2b,c | 0.3e-g | 6.9f | 5.0b-d | 1.4d |
| Hairy indigo | L ₁ | L ₂ | 101.1a,b | 6.4a-d | 5.4b,c | 0.3e-g | 26.2a,b | 17.4a | 4.9a-c |
| | L ₁ | L ₂ | 107.8a | 8.0a | 10.0a | 0.5d-g | 24.8a-c | 20.1a | 6.4a |
| Lab-lab | L ₁ | L ₂ | 86.0a-c | 8.5a | 5.7bc | 0.2fg | 20.9a-d | 10.9b | 2.9de |
| | L ₁ | L ₂ | 59.1b-d | 6.7a-c | 1.9c | 0.1g | 16.1b-f | 6.1b-d | 1.6e |
| Sesbania | L ₁ | L ₂ | 50.9c,d | 3.7b-d | 2.3b,c | 0.3e-g | 13.4d-f | 3.4c,d | 1.5e |
| | L ₁ | L ₂ | 58.6b-d | 5.2a-d | 2.7b,c | 0.5e-g | 12.4d-f | 3.9c,d | 1.9e |
| Brazilian stylo | L ₁ | L ₂ | 54.8c,d | 5.6a-d | 3.8bc | 0.6c-f | 15.4c-f | 7.8b-d | 1.9e |
| | L ₁ | L ₂ | 65.2a-d | 5.8a-d | 3.8bc | 0.2f,g | 17.9a-e | 9.9b,c | 2.3d,e |
| Cowpea | L ₁ | L ₂ | 85.1a-d | 8.8a | 5.5bc | 0.6b-f | 26.9a | 8.1b-d | 5.1ab |
| | L ₁ | L ₂ | 67.4a-d | 7.6a,b | 4.0b,c | 1.0a-d | 16.7a-f | 4.9b-d | 3.9a-d |
| Mean | L ₁ | L ₂ | 67.4 | 6.1 | 4.5 | 0.5 | 16.4 | 7.8 | 2.8 |
| | L ₁ | L ₂ | 60.9 | 5.8 | 4.3 | 0.5 | 13.9 | 7.4 | 2.9 |
| Significance | | | * | * | * | ** | ** | ** | ** |
| Species (S) | | | NS | NS | NS | NS | NS | NS | NS |
| PPFD (P) | | | NS | NS | NS | NS | NS | NS | NS |
| S × P | | | NS | NS | NS | NS | NS | NS | NS |

Values within a column followed by the same letter are not significantly different ($P < 0.05$, Tukey's test).

*, **, *Significant at 0.05 and 0.01 levels of probability, respectively.

^aL₁ = PPF₁ (Photosynthetic Photon Flux Density) of 200 μmol m⁻² s⁻¹; L₂ = PPF₂ of 400 μmol m⁻² s⁻¹.

Table 5.5 Influence of PPFD on transport of macronutrients in different species of leguminous cover crops

| Species | PPFD ^a | | | | | | | |
|-------------------|-------------------|---------|---------|---------|---------|---------|---------|---------|
| | N | P | S | Na | K | Ca | Mg | |
| Joint Vetch | L ₁ | 5.66c,d | 0.77a | 0.37c,d | 0.03e-h | 1.31c,d | 0.70c | 0.30c,d |
| | L ₂ | 5.85b-d | 0.68b | 0.33e-f | 0.01f-h | 1.24d,e | 0.67c,d | 0.32b,c |
| Sunhemp | L ₁ | 5.30d | 0.47e,f | 0.41b,c | 0.11b | 1.00g,h | 0.48e-g | 0.19g |
| | L ₂ | 5.31d | 0.54d,e | 0.41bc | 0.17a | 0.99g,h | 0.58d,e | 0.29c,d |
| Crotalaria ochro. | L ₁ | 6.79a,b | 0.56c,d | 0.54a | 0.10b,c | 1.28d | 0.53e,f | 0.24e,f |
| | L ₂ | 5.91b-d | 0.64bc | 0.51a,b | 0.09b-d | 1.23d,e | 0.66c,d | 0.35a,b |
| Showy crotalaria | L ₁ | 5.99b-d | 0.37h | 0.50a,b | 0.05d-g | 1.01g | 0.71c | 0.19g |
| | L ₂ | 6.33b,c | 0.41f-h | 0.48a,b | 0.04e-h | 1.05f,g | 0.75c | 0.21f,g |
| Hairy indigo | L ₁ | 5.59c,d | 0.36h | 0.29e-g | 0.02e-h | 1.45c | 0.96b | 0.27d,c |
| | L ₂ | 6.47b,c | 0.48e,f | 0.59a | 0.03e-h | 1.46b,c | 1.21a | 0.38a |
| Lab-lab | L ₁ | 3.85e | 0.39g,h | 0.20g,h | 0.01g,h | 1.03f,g | 0.47f-h | 0.12i,j |
| | L ₂ | 3.68e | 0.42f-h | 0.12h | 0.00h | 1.00g,h | 0.38h,i | 0.10j |
| Sesbania | L ₁ | 6.42b,c | 0.47e-g | 0.28e-g | 0.04e-h | 1.70a | 0.42g-i | 0.18g,h |
| | L ₂ | 7.67a | 0.69b | 0.35c-e | 0.06c-e | 1.62a,b | 0.51e-g | 0.25e |
| Brazilian stylo | L ₁ | 3.48e | 0.35h | 0.24e-g | 0.04e-h | 0.98g,h | 0.50e-g | 0.12i,j |
| | L ₂ | 4.26e | 0.38h | 0.25e-g | 0.02f-h | 1.17d-f | 0.65c,d | 0.15h,i |
| Cowpea | L ₁ | 3.46e | 0.36h | 0.23f-h | 0.03e-h | 1.09e-g | 0.33i,j | 0.21f,g |
| | L ₂ | 3.42e | 0.38h | 0.20g,h | 0.05d-f | 0.85h | 0.26j | 0.20g |
| Mean | L ₁ | 5.17 | 0.46 | 0.34 | 0.03 | 1.21 | 0.57 | 0.20 |
| | L ₂ | 5.43 | 0.51 | 0.36 | 0.04 | 1.14 | 0.63 | 0.25 |
| Significance | | | | | | | | |
| Species (S) | ** | ** | ** | ** | ** | ** | ** | ** |
| PPFD (P) | NS | ** | NS | NS | NS | ** | ** | ** |
| S × P | NS | ** | ** | NS | NS | ** | ** | ** |

Values within a column followed by the same letter are not significantly different ($P < 0.05$, Tukey's test).

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

^aL₁ = PPFD (Photosynthetic Photon Flux Density) of 200 μmol m⁻² s⁻¹; L₂ = PPFD of 400 μmol m⁻² s⁻¹.

with shoot dry weight in the order of $N = P > K > Ca = Mg > S > Na$. Hence, it can be concluded that N is the most yield limiting nutrient and Na is the least yield limiting nutrient for cover crops evaluated in this study. Cowpea, sesbania, lab-lab, and sunhemp produced good growth and higher nutrient uptake than other legumes at lower as well as at higher PPFD. Hence, these crop species appears to be suitable cover crops for tropical plantations crops with low PPFD.

Acknowledgments We thank S. Faulkner and J. Mascio for excellent technical support, J. Fisher for statistical analysis and Charles D. Foy, for critical comments. We thank following seed suppliers. Seeds of sunhemp, crotalaria ochroleuca, showy crotalaria, and lab-lab were received from Pirai seed company Av. Cassio paschoals Pado Vam; No 333, Piracicaba-SP Brazil; seeds of cowpea were received from Dr. Corival da Silva Embrapa Rice and Bean center GO Brazil; seeds of Brazilian style were received from Globo rural seed company, Av. Castello Branco 2177 Set Combra, Goania GO Brazil; seeds of joint vetch and hairy indigo were received from Adams-Briscoe Seed Co, Jackson GA and seeds of susbania were received from Dr Y. Li TREC – University of Florida, Homestead FL. Mention of trademark, proprietary product, or vender does not constitute a guarantee or warranty of the product by the U. S. Dept. of Agriculture and does not imply its approval to the exclusion of other products or venders that also may be suitable.

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