

Carbon dioxide and photosynthetic photon flux density effects on growth and mineral uptake of cacao

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Abstract

In recent years, carbon dioxide concentration [CO₂] in the atmosphere has risen to 370 μmol mol⁻¹, with levels expected to double by the end of the 21st century. A climatically-controlled greenhouse experiment was undertaken to assess the influence of [CO₂] and photosynthetic photon flux density (PPFD) on the growth, mineral nutrient uptake and mineral nutrient use efficiency parameters of cacao (*Theobroma cacao* L) in its early growth stages. Plants were grown in two greenhouses and maintained at two levels of [CO₂] (380 and 700 μmol mol⁻¹). In each greenhouse, three levels of PPFD (65, 190, 1050 μmol m⁻²s⁻¹) were achieved by constructing mini shade frames covered with various layers of plastic shade cloth. Plants were grown for 57 days. At all levels of PPFD, with few exceptions, increasing [CO₂] tended to increase shoot and root growth parameters (dry wt. of roots, stem and leaves, stem height, leaf area, shoot/root ratio, leaf area ratio and relative growth rate). At both [CO₂], increasing PPFD from 65 to 190 μmol m⁻²s⁻¹ increased shoot and roots growth, relative growth rate and net assimilation rate. At both [CO₂], PPFD of 1050 μmol m⁻²s⁻¹ was detrimental to growth and to mineral nutrient uptake parameters; however, its effects were more severe at 380 than 700 μmol mol⁻¹ of [CO₂]. At all PPFD with few exceptions, increasing [CO₂] increased the uptake of all mineral nutrients. With some exceptions, at both [CO₂] levels increasing PPFD increased nutrient influx (IN) for Na, B, Mn and Zn and decreased IN for other mineral nutrients. With some exceptions, at both [CO₂] levels increasing PPFD decreased nutrient transport (TR) for Na and S and increased TR for Mg, B, and Zn only. At both [CO₂] with the exception of nutrient use efficiency ratio (ER) for B, increasing PPFD increased ER for N, Na, S and Zn and decreased ER for other mineral nutrients. At all PPFD levels, with few exceptions, overall, increasing [CO₂] increased ER for N, Na, Mg, Cu, Mn and Zn and decreased ER for other mineral nutrients. Growth, mineral nutrient uptake parameters and nutrient use efficiency ratios in cacao were influenced by [CO₂] and PPFD. Overall, PPFD of 190 μmol m⁻²s⁻¹ appears to be a desirable light intensity and combined with increasing [CO₂] are beneficial in improving cacao growth and mineral nutrient uptake and use efficiency.

Key words: Cacao, *Theobroma cacao*, net assimilation rates, nutrient influx and transport, nutrient use efficiency ratio, relative growth rate.

Introduction

Botanically cacao (*Theobroma cacao* L) is considered to be a shade, rather than sun plant. In South and Central America cacao is mostly grown as an understory plant under various types of shade trees, and this results in its exposure to different levels of shade. The amount of sunlight falling on a cacao tree is known to affect its growth and yield¹. However, there is no universal agreement on the degree of shade required to maximize its production potential^{1,2}. Understory plants in tropical forests usually receive a photosynthetic photon flux density (PPFD) of between 5 and 25 μmol m⁻²s⁻¹ or 1 to 2% of that received at the canopy level³⁻⁶ and intermittently they also receive high levels of PPFD⁷. The canopy also reduces the red:far-red (R:FR) of light reaching the under story⁸ and may affect the efficiency with which the intercepted radiation is used in photosynthesis⁵. Saturating PPFD in cacao is around 250-400 μmol m⁻²s⁻¹^{9,10}, and 95% of the maximum photosynthesis known to occur¹⁰ at 200 μmol m⁻²s⁻¹.

The carbon dioxide concentration [CO₂] in the atmosphere has risen in the last 110 years to 370 μmol mol⁻¹ and is expected to reach around 700 μmol mol⁻¹ by the end of the 21st century¹¹. An increasing atmospheric [CO₂] is known to stimulate photosynthesis and biomass accumulation in a number of plant species¹²⁻¹⁵. However, most studies relating plant response to

elevated [CO₂] have only involved temperate plants and very little attention has been directed at responses of tropical plants such as cacao¹⁶. Limited data from greenhouse and laboratory studies with tropical plants indicate that elevated [CO₂] increases growth, photosynthesis and water use efficiency¹⁶. Effects of increased [CO₂] on plant morphological development have received considerably less attention. In tree species, increasing [CO₂] increased plant dry matter accumulation and mean mass per unit leaf¹⁷. Higher dry weights and net CO₂ assimilation were reported for nine tropical species subjected to elevated (2x ambient) [CO₂]¹⁵. Enhanced biomass accumulation under elevated [CO₂] creates a higher demand for nutrients. Nutrient supply in tropical soils lags behind the increased plant demand.

Many agricultural soils of the world are deficient in one or more of the essential nutrients to support healthy and productive plant growth^{18,19}. Mineral stress problems in various soil orders of the world are due to the nature of parent materials and climatic factors²⁰. Years of cultivation, loss of nutrients through erosion and leaching and decreased use of nutrient inputs have contributed to accelerated soil degradation and exhaustion of available essential nutrients in tropical soils^{18,21,22}, especially soils under cacao¹. Although cacao is grown on a wide range of soils, most of these soils are nutrient poor and slightly acidic.

Therefore, anticipated higher [CO₂], coupled with low levels of soil nutrients and their supply, subjects cacao to severe nutrient stress. Lack of appropriate levels of essential nutrients in plants results in expression of nutrient deficiencies, and eventually this leads to a decline in yield potentials. Deficiencies of Ca, Mg, Zn and Fe in cacao have been widely reported in many regions of the world²³. Phosphorus is the major limiting nutrient in almost all soils in which cacao is grown²⁴. Higher nutrient use efficiency in cacao could reduce fertilizer input cost, decrease the rate of nutrient losses and enhance crop yields. The reported concentrations of macro- and micronutrients in cacao leaves ranges from severely deficient to normal^{23, 25-29}. Very little information is available on the effects of light intensity and elevated [CO₂] and their interactions on growth and nutrient uptake parameters in cacao. Based on the literature cacao appears to have higher nutrient requirements than other tropical perennials when grown on acid low fertility soils³⁰. The objectives of this study were to assess the effects of [CO₂] and photon flux density (PPFD) and their interactions on growth and physiological traits (shoot and root growth parameters, relative growth rates, net assimilation rate), macro- and micronutrient nutrition (uptake, influx, transport) and nutrient use efficiency ratios in cacao.

Materials and Methods

Generation and transplant of seedlings: In this experiment cacao Comum plants were used. Comum cacao pods were received by airfreight from the Alimirante Cacao Research Center in Itajuípe, Bahia, Brazil. Seeds from cacao pods were separated and seed coats were removed. Seeds were soaked in 10% chlorine bleach (sodium hypochlorite) for two minutes, washed twice in DI-water, and then soaked for two min. in 90% ethanol and washed twice in DI-water. Seeds were germinated on sterile moist filter paper for 48 h at 25°C. Seeds with 5 mm radicals were planted in 7.6 cm plastic pots in a mixture of sand and ProMix (1:1 volume) and watered as needed. Seedlings were grown under greenhouse conditions. After 14 days of growth plants were transferred to 3.8 L black plastic pots containing 2.2 kg mixture of sand: perlite: ProMix (2:2:1 volume) with adequate bottom drainage. One seedling was planted in each pot. At the time of planting to provide supplemental nutrients, each kg medium received 2.5 g of Multicote 6 fertilizer (TRI-PRO, Apopka, FL) containing (%) 15 N, 6.6 P, 12.5 K, 0.6 Mg and 0.15 Fe as FeEDTA. Plants were transferred to greenhouses on the 7th d after potting and on the second day N 170 mg kg⁻¹ as urea and 1.4 g kg⁻¹ of Fer-a-gro (A-FEC F & C Co., Homestead, FL) containing (%) 4 S, 2.64 Mg, 0.011 B, 1.59 Fe, 1.53 Mn, 0.001 Mo and 0.9 Zn were added as a nutrient drench. Pots were watered on a daily basis to maintain water content at field capacity.

CO₂ and PPFD treatments: Two identical air-conditioned greenhouses (13.5 m² each) with day/night temperature of 28/25°C were used for the duration of the experiments. Daytime air temperatures were maintained for 12 h per day beginning at 6 AM. The greenhouses transmitted approximately 65% of the incident PPFD on a daily basis. One greenhouse contained near ambient CO₂ (380 μmol mol⁻¹) and the second had elevated CO₂ (700 μmol mol⁻¹). The CO₂ concentration of 700 μmol mol⁻¹ was controlled 24 h by a WMA2 infra-red gas analyzer (PP Systems, Haverhill, MA) which injected CO₂ when the levels fell below the desired [CO₂] level. Within each greenhouse, electrical fans

continuously circulated the air at an air speed of 0.5 m/s over the plants. A data logger (21x, Campbell Scientific, Logan, UT) recorded the PPFD, temperature and [CO₂] in both the greenhouses at 30-s intervals. Mean daily air temperatures were always within 0.2°C in the two greenhouses, and the data were analyzed assuming that [CO₂] was the only environmental factor differing between the greenhouses. Ambient night-time CO₂ concentration values were higher than 380 μmol mol⁻¹ at this site due in part to low wind speed and stable atmospheric conditions. In each greenhouse two mini chambers were utilized to achieve different PPFD levels. Mini chambers were constructed with 2 cm (3/4 inch) diameter PVC pipe with overall dimensions of 60W cm x 120L cm x 76H cm. To achieve two different levels of shading, tops and sides of mini chambers were covered with plastic shade cloth. Single-ply cloth for less shade and double-ply cloth for higher shade was employed. Plants were also placed on benches with no shade. On every 7th day at midday, PPFD was determined by Li-Cor LI-190S Quantum sensor (Li-Cor Inc., Lincoln, NB) in mini chambers and in greenhouses. The average PPFD achieved with such mini chamber arrangement and the greenhouse were 65±25, 190±46 and 1050±260 μmol m⁻² s⁻¹ for high shade, medium shade and no shade respectively.

The experiment was terminated after plants had been in glasshouses for 57 d. Roots and shoots were separated and washed with deionized water. Leaves were separated, leaf area was determined by Li-Cor model 300 leaf area meter (Li-Cor Inc., Lincoln, NB) and stem height was recorded. Shoots and roots were blotted dry, oven dried at 70°C for 5 d and weighed. Dried shoot samples were ground to pass through 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 use of modified methods suggested by Wolf³¹. Plant samples were wet digested in conc. sulphuric acid and 30% hydrogen peroxide. A Gilford STASAR II spectrophotometer was used to determine N, S, P, and B, and a Perkin Elmer Analyst 400 Atomic Absorption Spectrometer was used to determine K, Ca, Mg, Na and micronutrients. Plant samples were digested in a muffle furnace at 600°C with magnesium nitrate and dissolved in 1:1 HCl, S concentrations were determined by a colorimetric method by using a Gilford STASAR II spectrophotometer.

Determination of growth and nutrient uptake parameters: Plant shoot, root and leaf growth and nutrient influx, transport and use efficiency ratio parameters were calculated as follows:

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 = [1/SLA] (LMA, g/cm²)

Leaf/Shoot Ratio (L/S) = [Leaf dry wt/Shoot dry wt.]

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

Relative Growth Rate (RGR) = [ln (Wt₂/Wt₁) / (T₂-T₁)], where Wt is total weight (shoot + root), T is time in days, 1 and 2 refers to at initial and final harvest.

Net assimilation Rate (NAR) = [RGR/LAR]

Nutrient Influx (IN) = [(U₂ - U₁) / (T₂-T₁)] • [(lnWr₂-ln Wr₁) / (Wr₂- Wr₁)], where U refers to elemental content in shoot (mmol/plant) and T is time in seconds, subscripts 1 and 2 refer to initial

and final harvest time.

Nutrient Transport (TR) = $\{(U_2 - U_1) / (T_2 - T_1)\} \cdot \{(\ln W_{s_2} - \ln W_{s_1}) / (W_{s_2} - W_{s_1})\}$

Nutrient Use Efficiency Ratio (ER) = [mg of Ws / mg of any given element in shoot]

Details of the methods used for determination of plant growth, nutrient uptake and physiological parameters were described by Baligar³², Baligar and Barber³³, Baligar et al.³⁴, Bunce³⁵ and Ziska and Bunce³⁶. A split plot design was used, where [CO₂] levels were main treatments, and PPFD levels were sub-treatments; each treatment had six replicates. Results were subjected to analysis of variance using general linear model (GLM) procedures of SAS (Ver. 8.1, SAS Institute, Cary, NC).

Results and Discussion

Growth parameters: Cacao growth and development are profoundly influenced by a complex of genetic, physiological and morphological determinants and their interactions with environmental variables, such as carbon dioxide concentration [CO₂] and level of light intensity^{1,2}. In the present experiment [CO₂], PPFD and their interaction significantly influenced the stem ht. Dry wt of leaves, stem ht, and R/S were significantly influenced by PPFD (Table 1).

At both [CO₂], increasing PPFD from 65 to 190 $\mu\text{mol m}^{-2}\text{s}^{-1}$ tended to increase biomass accumulation in roots, leaves, stem and shoot, and stem ht. Such an increase in biomass accumulation resulted in increased RGR. At both [CO₂], PPFD of 1050 $\mu\text{mol m}^{-2}\text{s}^{-1}$ was detrimental to shoot, root and leaf growth, but its effect was more severe at ambient [CO₂]. Saturating PPFD, for photosynthesis in cacao has been reported to be about 400 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and 95% of the maximum photosynthesis is known to occur at 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$ ¹⁰. Hutcheon⁹ reported that in cacao the maximum light saturation point was 250-300 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (about 15% of full midday sunlight). At both [CO₂] increasing PPFD to 190 $\mu\text{mol m}^{-2}\text{s}^{-1}$ produced relatively higher dry matter allocation to the roots than shoots and this in turn led to higher root/shoot ratio and RGR. At both [CO₂] increasing PPFD's significantly increased NAR.

Overall, at all levels of PPFD, increasing [CO₂] tended to increase dry weight of leaves, stem and roots, stem height, shoot/root ratio and RGR. With the exception of PPFD 1050 $\mu\text{mol m}^{-2}\text{s}^{-1}$, NAR decreased with increasing [CO₂]. Effects of elevated [CO₂] on morphological development of tropical plants has received considerably less attention than that of subtropical and temperate region plants. In tree species increasing [CO₂] increased plant dry matter accumulation and mean mass per unit leaf¹⁷. Increases in dry weight and net CO₂ assimilation were reported for nine tropical species subjected to elevated (2x ambient) CO₂ concentrations¹⁵. Bunce³⁵ subjected seven C₃ crop and three C₃ weed species to 360 and 700 $\mu\text{mol mol}^{-1}$ [CO₂]. At elevated CO₂ the dry mass was highly correlated with the RGR. Relative increase in RGR was highly correlated with a relative increase in NAR. Correlations between NAR and LAR can conceivably be either positive or negative³⁷. Results of the current study with cacao support these earlier findings with other species of plants.

At both the [CO₂], increasing PPFD significantly decreased leaf area, specific leaf area (SLA), leaf/shoot ratio and leaf area ratio (LAR); however, leaf mass/unit leaf area (LMA) was significantly increased (Table 2). Although the growth of C₃ plants

generally responds positively to increased [CO₂] above the current ambient concentration of about 370 $\mu\text{mol mol}^{-1}$ ³⁸, the increase in growth usually is not as large as would be predicted from the increase in photosynthesis^{39,40}. This is often attributed to a reduction in LAR at elevated [CO₂]⁴¹. Leaf area ratio (LAR) shows variable responses depending on growth conditions¹⁶. In the current study, at lower PPFD's increasing [CO₂] increased LAR, however, at PPFD of 1050 $\mu\text{mol m}^{-2}\text{s}^{-1}$ increasing [CO₂] tend to reduce LAR. Change in leaf area per plant appears to be a better predictor of growth than change in maximum assimilation rate, change in leaf area ratio or the product of the two¹⁶.

At both [CO₂] levels increasing PPFD to 1050 $\mu\text{mol m}^{-2}\text{s}^{-1}$ resulted in reduction of most of the growth parameters. Prolonged exposure to high light intensities is known to damage the photosynthetic mechanism of cacao leaves¹⁰. Serrano and Biehl⁴² have shown that cacao is unable to adapt to high light intensities. In unshaded plantations cacao trees showed signs of photoinhibitory stress and with reduced water supply and nutrients such stress can reduce productivity.

Mineral nutrient uptake: Tropical soils are often nutrient poor¹⁸, and most of the nutrient pool in tropical forests is in the plant biomass itself⁴³. Information is lacking on interactions of elevated [CO₂], light, water and nutrients on growth of tropical plants¹⁶. With few exceptions at all the PPFD, overall increasing [CO₂] tended to increase the uptake of all mineral elements (Table 3). Higher [CO₂] increased the demand for mineral nutrient requirement due to enhanced dry matter accumulation.

At ambient [CO₂] of 380 $\mu\text{mol mol}^{-1}$ increasing PPFD decreased uptake of N, Ca, Na, P, S, and Cu. However, uptake of other mineral elements increased with increasing PPFD from 65 to 190 $\mu\text{mol m}^{-2}\text{s}^{-1}$, and further increase in PPFD reduced the uptake of these minerals. Such reduction in mineral uptake could be attributed to a reduction in dry matter accumulation at higher level of PPFD, and that contributed to reduced nutrient demand. Generally, shaded cacao contains higher levels of N and K than unshaded trees, which had higher levels of P, Ca and Mg³⁰. Beneficial effects of fertilization on sustaining cocoa bean yields in reduced shade is well documented^{24,44}.

At elevated [CO₂] of 700 $\mu\text{mol mol}^{-1}$ increasing PPFD increased uptake of Cu, Mn, and Zn and decreased uptake of Na and S. Uptake of other mineral nutrients increased with increase in PPFD up to 190 $\mu\text{mol m}^{-2}\text{s}^{-1}$, and further increase in PPFD reduced the uptake of these nutrients. Deficiencies of N, K, Ca, Mg Zn, B and Fe in cocoa have been widely reported in many regions of the world^{23,30}. Such mineral deficiency is mainly due to low fertility of soils where cacao is grown. Loss or reduction of shade under elevated [CO₂] might induce additional nutrient disorders in cacao.

Overall, [CO₂] had significant effects on uptake of K, Ca, and S but PPFD only had significant effect on uptake of Na and S (Table 3). With anticipated increase in global [CO₂] and loss of shade, nutrient management in perennial cacao plantation will be very critical in meeting plant nutrient demands and supporting cacao production potentials. Management of soil nutrients to meet crop demands becomes very challenging in the cultivation of a long duration plantation crop such as cacao grown on infertile tropical soil. With a further reduction in shade, nutrient management becomes even more critical.

Table 1. Shoot and root growth, RGR and NAR as influenced by carbon dioxide concentration [CO₂] and PPFD.

[CO ₂] (μmol mol ⁻¹)	PPFD (μmol m ⁻² s ⁻¹)	Dry weight (g plant ⁻¹)					Stem ht (cm)	R/S ratio	S/R ratio	RGR ^a x 10 ⁻²	NAR ^b x 10 ⁻⁴
		Shoot			Root	Total					
		leaves	stem	total	plant						
380	65	5.21	1.74	6.95	1.84	8.79	26.42	0.27	3.80	4.00	2.60
	190	5.46	2.11	7.57	2.48	10.05	27.20	0.32	3.22	4.20	3.31
	1050	3.82	1.78	5.59	2.04	7.64	21.50	0.37	2.78	3.90	3.53
700	65	5.42	2.06	7.48	1.89	9.37	31.23	0.26	4.01	4.20	2.47
	190	6.28	1.89	8.17	2.25	10.41	32.70	0.28	3.68	4.40	3.05
	1050	4.62	2.13	6.74	2.23	8.97	23.83	0.32	3.17	4.10	4.37

Significance

[CO ₂]	NS	NS	NS	NS	NS	**	NS	NS	NS	NS
PPFD	*	NS	NS	NS	NS	**	*	**	NS	**
[CO ₂] X PPFD	NS	NS	NS	NS	NS	**	NS	NS	NS	NS

^aRGR = g g⁻¹ d⁻¹; ^bNAR = g cm⁻² d⁻¹; **, * Significant at 0.05 and 0.01 levels of probability, respectively; NS = Not significant.

Table 2. Leaf parameters as influenced by carbon dioxide concentration [CO₂] and PPFD.

[CO ₂] (μmol mol ⁻¹)	PPFD (μmol m ⁻² s ⁻¹)	Leaf Area (cm ²)	SLA (cm ² g ⁻¹)	LMA (g cm ⁻² x 10 ⁻³)	L/S	LAR (cm ² g ⁻¹)
380	65	1366.00	268.03	3.77	0.75	160.07
	190	1291.37	243.71	4.60	0.73	135.61
	1050	836.62	218.48	4.60	0.69	109.56
700	65	1512.70	281.82	3.56	0.72	170.21
	190	1493.66	240.97	4.16	0.76	143.36
	1050	852.90	187.39	5.40	0.69	98.44

Significance

[CO ₂]	NS	NS	NS	NS	NS	NS
PPFD	**	**	**	**	*	**
[CO ₂] X PPFD	NS	NS	*	NS	NS	NS

**, * Significant at 0.05 and 0.01 levels of probability, respectively; NS = Not significant.

Table 3. Nutrient uptakes as influenced by carbon dioxide concentration [CO₂] and PPFD^a.

[CO ₂] (μmol mol ⁻¹)	PPFD (μmol m ⁻² s ⁻¹)	N	K	Ca	Mg	Na	P	S	B	Cu	Fe	Mn	Zn
380	65	168.66	84.99	60.75	43.91	11.54	8.78	6.92	192.28	53.94	485.93	1274.84	508.95
	190	159.80	103.05	50.29	49.53	8.45	8.89	6.67	221.88	53.50	501.21	1531.84	621.58
	1050	114.20	82.20	40.42	38.23	3.93	7.49	4.71	154.29	45.63	410.41	1298.70	444.31
700	65	158.00	112.18	76.80	47.12	11.07	9.26	10.56	202.10	44.38	538.68	1127.38	498.64
	190	165.96	145.61	85.75	55.04	8.02	10.42	8.68	270.76	56.94	534.67	1638.63	646.55
	1050	150.86	111.82	77.91	44.61	5.43	9.81	6.74	198.66	69.05	470.61	1763.97	731.56

Significance

[CO ₂]	NS	**	**	NS	NS	NS	**	NS	NS	NS	NS	NS	NS
PPFD	NS	NS	NS	NS	**	NS	*	NS	NS	NS	NS	NS	NS
[CO ₂] X PPFD	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

^aMacronutrients (N, K, Ca, Mg, Na, P, S) in mg plant⁻¹ and micronutrients (B, Cu, Fe, Mn, Zn) in μg plant⁻¹; **, * Significant at 0.05 and 0.01 levels of probability, respectively; NS = Not significant.

Mineral nutrient influx (IN) and transport (TR): At both [CO₂] levels increasing PPFD tended to decrease IN for N, K, Ca, Mg, P, S, Cu and Fe, however, effects were only significant for N, Na and S (Table 4). With the exceptions of IN for N, Na, Cu, and Mn at PPFD of 65 μmol m⁻² s⁻¹, overall increasing [CO₂], at all PPFD levels, increased IN for other mineral elements, with significant increases for K, Ca and S.

At ambient [CO₂], TR for most mineral nutrients decreased with increasing PPFD; however, TR tended to increase for K, Mg, B,

and Mn (Table 5). At elevated [CO₂], increasing PPFD decreased TR for K, Na, S and Fe but enhanced TR for other mineral nutrients. Invariably, at all PPFD increasing [CO₂] decreased TR for N, Ca, Na, and Zn and increased TR for other elements. Overall, [CO₂] had significantly affected TR for K, Ca, and S; however, PPFD only had a significant effect on TR for Na and S.

Very little information is available on the influx and transport of essential nutrients in cacao; however, compared with other tropical perennial crops that are capable of growing on acid infertile soils, cacao has higher nutrient requirements³⁰. On an average 1000 kg of cocoa beans contain about 30 kg of N, 4 kg of P, 33 kg of K, 9 kg of Ca and 6 kg of Mg². These nutrients have to be absorbed by roots, subsequently transported to the shoot and remobilized to the beans. Anticipated increased levels of [CO₂] and enhanced light intensities due to loss of the shade trees could increase demands for nutrients by cacao in soils that are already low in most of essential nutrients. Genetic and physiological components of plant and their interactions with environmental variables profoundly affect the ability of plants to acquire, transport and utilize absorbed nutrients^{18, 45-47}.

Mineral nutrient use efficiency ratios (ER):

The ER values are useful in assessing the ability of plants to use absorbed nutrients efficiently or non-efficiently, especially in degraded and low fertility tropical soils. At both [CO₂], increasing PPFD increased ER for N, Na, S and Zn (Table 6). However, with exception of ER for B, at both [CO₂] levels, increasing PPFD decreased ER for other mineral nutrients. At all PPFD, with few exceptions, increasing [CO₂] levels, increased ER for N, Na, Mg, Cu, Mn and Zn and decreased ER for other mineral nutrients.

Overall, increasing levels of [CO₂] significantly affected ER for K, Ca and S, and PPFD significantly affected ER of K, Na, P, S, Cu, Mn and Zn. Interactions of [CO₂] and PPFD significantly affected ER of N and Mg only. Mineral nutrient use efficiencies are known to be under genetic and physiological control and are modified by plant interaction with environmental variables^{19, 45-47}. Intensive cultivation of soils with steep slopes under perennial plantation crops such as cacao and nonexistent or inadequate fertilizer inputs, invariably lead to degradation of land and lowering of

Table 4. Nutrient influx (IN, pmol·g⁻¹ root·sec⁻¹) as influenced by carbon dioxide concentration [CO₂] and PPFD.

[CO ₂] (μmol·mol ⁻¹)	PPFD (μmol·m ⁻² ·s ⁻¹)	N	K	Ca	Mg	Na	P	S	B	Cu	Fe	Mn	Zn
380	65	3126	520	411	501	151	50	58	4.82	0.20	1.85	5.14	1.65
	190	2444	561	271	474	84	43	45	5.02	0.16	1.61	5.50	1.85
	1050	1850	481	251	406	45	37	35	3.60	0.15	1.44	5.02	1.30
700	65	2891	874	516	524	147	55	93	5.20	0.51	2.17	4.33	1.65
	190	2681	814	543	554	88	57	66	6.27	0.19	1.91	6.14	2.00
	1050	2475	663	499	452	61	55	50	4.45	0.24	1.69	6.93	2.42

Significance

[CO ₂]	NS	**	**	NS	NS	NS	**	NS	NS	NS	NS	NS	NS
PPFD	*	NS	NS	NS	**	NS	**	NS	NS	NS	NS	NS	NS
[CO ₂] X PPFD	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

*,** Significant at 0.05 and 0.01 levels of probability, respectively. NS = Not significant.

Table 5. Nutrient transport (TR, pmol·g⁻¹ shoot·sec⁻¹) as influenced by carbon dioxide concentration [CO₂] and PPFD.

[CO ₂] (μmol·mol ⁻¹)	PPFD (μmol·m ⁻² ·s ⁻¹)	N	K	Ca	Mg	Na	P	S	B	Cu	Fe	Mn	Zn
380	65	749	125	98	120	36	12	14	1.16	0.05	0.44	1.22	0.39
	190	667	153	75	129	24	12	12	1.34	0.04	0.44	1.50	0.50
	1050	553	143	75	121	13	11	10	1.08	0.04	0.43	1.50	0.39
700	65	661	208	115	119	34	12	21	1.19	0.03	0.50	0.97	0.37
	190	658	203	133	137	22	14	16	1.52	0.06	0.47	1.49	0.48
	1050	681	182	138	125	17	15	14	1.23	0.07	0.46	1.94	0.67

Significance

[CO ₂]	NS	**	**	NS	NS	NS	**	NS	NS	NS	NS	NS	NS
PPFD	NS	NS	NS	NS	**	NS	*	NS	NS	NS	NS	NS	NS
[CO ₂] X PPFD	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS

*,** Significant at 0.05 and 0.01 levels of probability, respectively. NS = Not significant.

Table 6. Nutrient use efficiency ratios (ER, mg shoot/mg element in shoot) for nutrients in shoots as influenced by carbon dioxide concentration [CO₂] and PPFD.

[CO ₂] (μmol·mol ⁻¹)	PPFD (μmol·m ⁻² ·s ⁻¹)	N	K	Ca	Mg	Na	P	S	B	Cu	Fe	Mn	Zn
380	65	41.6	82.2	117.7	159.4	615.9	808.2	1003.4	3.89	13.50	1.51	0.56	1.38
	190	47.1	73.0	162.0	152.7	1059.5	858.1	1170.0	3.48	14.20	1.59	0.50	1.22
	1050	49.5	67.9	141.5	147.2	1478.8	753.7	1214.9	3.66	12.40	1.38	0.45	1.30
700	65	47.9	73.0	118.2	169.9	691.0	853.6	803.6	3.69	17.00	1.42	0.70	1.55
	190	50.5	59.9	95.7	150.9	1095.1	825.8	941.9	3.12	14.70	1.58	0.58	1.36
	1050	45.0	60.8	87.3	153.3	1318.8	703.2	1000.0	3.71	10.30	1.45	0.43	0.99

Significance

[CO ₂]	NS	**	**	NS	NS	NS	**	NS	NS	NS	NS	NS	NS
PPFD	NS	**	NS	NS	**	*	**	NS	*	NS	**	**	**
[CO ₂] X PPFD	**	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

*,** Significant at 0.05 and 0.01 levels of probability, respectively. NS = Not significant.

fertility and productivity. World wide elemental deficiencies for essential macro- and micronutrients (N, P, K, Ca, Mg, Mn, Zn, Cu, Fe, Mo, Si, B) and toxicities (Al, Mn, Fe, Na, Se, Cl) have been reported¹⁹. Plants that have high ER values for essential nutrients might grow well and produce higher yields when grown on infertile soils. Anticipated increase in [CO₂], coupled with reduced shade, might alter the ability of cacao to utilize absorbed nutrients more efficiently. Such changes might lead to increased fertilizer inputs to maintain yield potential, thereby increasing the cost of cacao production.

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