Agricultural and Forest Meteorology, 55 (1991) 15–21
Elsevier Science Publishers B.V., Amsterdam

Influence of environmental factors on photosynthesis in cocoa trees*

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(Received 23 April 1990; revision accepted 15 November 1990)

ABSTRACT

Balasimha, D., Daniel, E.V. and Bhat, P.G., 1991. Influence of environmental factors on photosynthesis in cocoa trees. Agric. For. Meteorol., 55: 15–21.

The photosynthesis of cocoa (*Theobroma cacao* Linn.) as influenced by light, temperature and vapour pressure deficit (VPD) was studied in the field. Net photosynthetic rate (P_N), transpiration rate and stomatal conductance showed significant seasonal variations. P_N was highest during periods of low evaporative demand (low VPD). Diurnal patterns of these parameters indicated transient midday water deficits which reduced P_N. Optimum temperature for P_N was 31–33°C and light saturation occurred at 400 μmol m^{-2} s^{-1}. The CO_2 compensation concentration was 100 ppm. Drought-tolerant accessions maintained higher leaf water potential than drought-susceptible types in dry months. There was no significant difference in P_N between tolerant and susceptible accession types.

INTRODUCTION

Environmental variables influence stomatal responses and net photosynthetic rates (P_N) in virtually all crops (Raschke, 1975; Farquhar and Sharkey, 1982; Schulze, 1986), but information on the photosynthetic characteristics of tropical tree crops is very scanty. Stomatal regulation and/or P_N in relation to climatic factors have been studied in coffee (Nunes, 1988), coconut (Kasturi Bai et al., 1988) and tea (Square and Callander, 1981). The influence of light (Raja Harun and Hardwick, 1988a), vapour pressure deficit (VPD), temperature (Raja Harun and Hardwick, 1988b) and water stress (Joly and Hahn, 1989) on cocoa seedlings have been reported.

In southern India, cocoa (*Theobroma cacao* Linn.) is cultivated as a mixed crop with arecanut (*Areca catechu* Linn.) palms. During the summer months the weather is dry for 3–5 months, with high evaporative demand resulting in soil and atmospheric drought of varying degrees of severity, depending on

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0168-1923/91/$03.50

rainfall pattern, cropping system and irrigation. Arecanut to a considerable extent, and coconut on a limited scale, are raised as irrigated crops; the environmental conditions in this region being favourable for cocoa growth (Shama Bhat, 1988). Balasimha and Rajagopal (1988) found that the stomatal conductance in cocoa is reduced by photosynthetically active radiation (PAR), relative humidity (RH) and soil moisture stress, an effect which improves water conservation. Drought tolerance in cocoa is mainly attributable to effective stomatal regulation, which results in decreased transpirational water loss (Balasimha et al., 1988). However, efficient stomatal closure may reduce carbon assimilation (Jones, 1979). To obtain a complete picture, it was necessary to study the impact of microclimatic variables on P_N in cocoa trees during the season and through the day.

MATERIALS AND METHODS

The location, soil characteristics and meteorological data for the Regional Station have been given in an earlier paper (Balasimha et al., 1985). The cocoa trees used in the present study (planted in 1970), were grown in the field in a mixed garden with arecanut palms. All the measurements were done in the field using intact leaves. Eight trees belonging to drought tolerant accessions (NC 23, NC 29, NC 31, NC 39, NC 42 and Amel×Na 33) and eight trees belonging to susceptible accessions (NC 24, NC 30, NC 52, NC 55, Redaxil, PA7×Na 32 and Amel×Na 32) were used for these investigations (Balasimha et al., 1988). Each tree was fertilized annually with 100 g N, 40 g P_2O_5 and 140 g K_2O and irrigated every 10 days during dry months.

Measurements of light (PAR), temperature (T_{air}), VPD, P_N, stomatal conductance (g_s) and transpiration rate (E) were made on three to five mature flushes per tree of the outer canopy using a Li-6200 portable photosynthetic system as described (Li-Cor Inc., 1987). In each case, fully expanded, healthy third or fourth leaves from the distal portion of the most recently hardened flush (representing approximately 1 month of growth) were used. This was done with a 1 l leaf chamber enclosing up to 30 cm^2 leaf area and equilibrated for 1–2 min. Two observations were recorded for each leaf. Water use efficiency (WUE) was calculated as the ratio of CO_2 assimilated to water transpired. Leaf water potential (ψ) was measured with a Scholander pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA) and soil moisture content was determined gravimetrically. Soil moisture was measured in three replicates at 0–50 cm depth and 50 cm distance from the cocoa tree. The soil is at field capacity at about 20% water content. All the measurements were made between 10 and 12 h except in the diurnal study.

CO_2 compensation studies were done by gradually decreasing the CO_2 in the chamber by scrubbing air through soda lime after enclosing the leaf. After 1–2 min of equilibration at each step, P_N was measured. The procedure was repeated until the compensation point was reached. The inter-cellular CC concentration (C_i) was computed in the Li-6200 using initial values of P_N, I ambient CO_2 concentration (C_a), and leaf resistance.

RESULTS AND DISCUSSION

The agrometeorological variables recorded during the season are given i Table 1. PAR, temperature, daily pan evaporation and VPD were higher i dry months (December, February, April and May) than in wet months (Jun and October). Soil moisture content gradually decreased during dry month: despite irrigation, because of a higher rate of evaporation from the soil sur

TABLE 1

Microclimatic variables recorded in the leaf chamber for the months February to December

Month	PAR (μmol m^{-2} s^{-1})	T_{air} (°C)	VPD (kPa)	Daily pan evaporation[1] (mm)	Soil moisture (%
February	550	31.7	2.48	4.6	16.1
April	589	35.3	2.89	6.1	14.7
May	526	35.7	2.96	6.4	14.0
June	333	31.9	1.71	5.5	16.3
October	423	31.9	1.14	3.4	16.6
December	565	33.1	2.79	5.0	15.3

[1] Recorded at the meteorological observatory of the Central Plantation Crops Research Institute, Regional Station, Vittal.

TABLE 2

Seasonal changes in P_N and other parameters

Parameter	Accession type	Month					Mean	LSD	
		Feb.	Apr.	May	Jun.	Oct.		Accession	Season
P_N	Tolerant	3.47	1.98	2.16	3.50	4.17	3.06	0.48	0.76**
(μmol m^{-2} s^{-1})	Susceptible	2.41	2.48	2.20	2.73	3.89	2.74		
g_s	Tolerant	0.14	0.07	0.07	0.18	0.27	0.15	0.03	0.04**
(mol m^{-2} s^{-1})	Susceptible	0.10	0.09	0.08	0.14	0.31	0.14		
E	Tolerant	2.77	1.91	2.44	1.82	3.54	2.50	0.53	0.85**
(mmol m^{-2} s^{-1})	Susceptible	1.86	2.39	2.45	1.84	5.37	2.78		
WUE	Tolerant	1.31	1.03	0.90	2.10	1.25	1.32	0.26	0.41**
(μmol CO_2/$mmol^{-1}$ H_2O)	Susceptible	1.31	1.03	0.91	1.76	0.88	1.18		
ψ (−MPa)	Tolerant	0.55	0.69	0.93	0.40	0.63	0.64	0.06*	0.10**
	Susceptible	0.54	0.91	1.03	0.43	0.70	0.73		

*Significant at $P=0.05$; **significant at $P=0.01$.

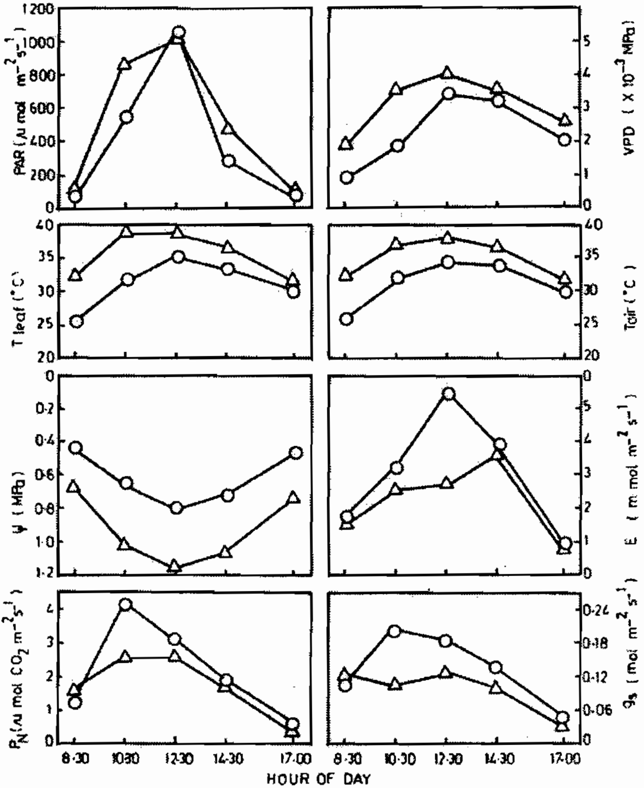

Fig. 1. Diurnal pattern of climatic factors, P_N and related parameters in December (○) an April (△). Values are means of six trees with the SE represented by vertical bars whenever i exceeds the circles.

face (Table 1). The wet period is from June to October; observations on microclimatic and plant variables could be made only during June and October

With the onset of monsoon rains in June, the plants were able to recove fully from water stress. Differences in P_N between drought-tolerant and susceptible accessions were not significant, but monthly values were significantl different (Table 2). Higher P_N values coincided with higher ψ values. Balasimha et al. (1988) indicated that cocoa effectively conserves water by stomatal closure; this view was supported by lower levels of g_s during the dr season (Table 2). As a result of this mechanism, drought-tolerant accession had higher ψ values during dry months. WUE also showed significant seasonal differences (Table 2).

Diurnal patterns of P_N and related parameters were studied in the months of December and April (Fig. 1). P_N and g_s were highest at 10:30 h and declined towards midday and the afternoon. The stressed plants had lower P_N and g_s values. The lowest value of ψ was recorded at midday, after which it recovered. At midday, the highest levels of PAR and VPD were recorded (Fig. 1). The decrease in g_s was more pronounced in April when both soil and atmospheric moisture was low and demand for water was high. Similar diurnal patterns have been reported in other tree crops (Bielorai and Mendel, 1969; Squire and Callander, 1981).

Stomata normally close in response to increasing VPD which is sensed by the leaf (Jarvis, 1980). The responses of P_N become even clearer when it is plotted against VPD (Fig. 2). Maximum P_N was recorded up to a VPD of 1.8 kPa; thereafter P_N declined. A reduction in g_s with higher VPD values has been reported in several crops (Raschke, 1975; West and Gaff, 1976; Squire and Callander, 1981; Guehl and Aussenac, 1987; Balasimha and Rajagopal,

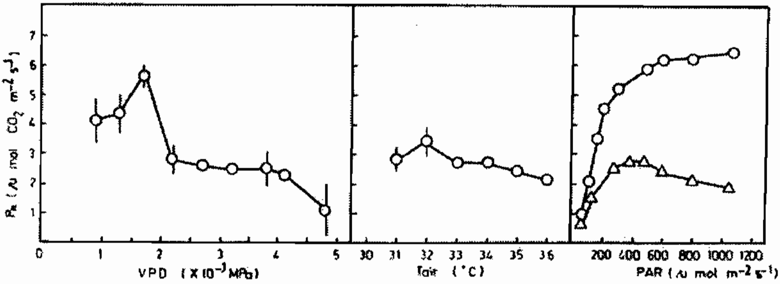

Fig. 2. Effect of VPD, T_{air} and PAR (October, ○; April, △) on P_N in cocoa leaves.

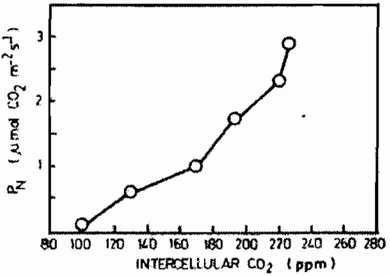

Fig. 3. Relation of P_N to C_i in cocoa leaves.

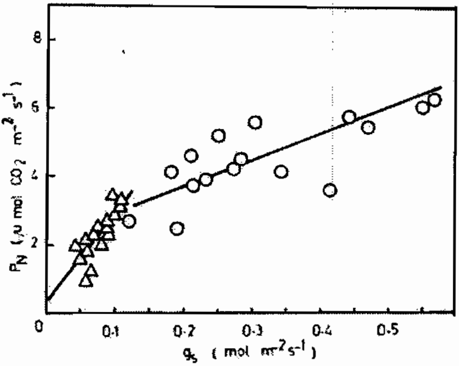

Fig. 4. Relation of P_N to g_s in cocoa leaves during October (○, $r=0.54$ at $P=0.05$) and April (△, $r=0.92$ at $P=0.01$).

1988; Kasturi Bai et al., 1988). The depression in P_N was principally due to lowered g_s. Temperature also had an effect on P_N, being optimum at 31–33°C, which is characteristic of tropical species grown in warm humid tropics (Fig. 2). Light saturation of P_N occurred at a PAR of 400 μmol m^{-2} s^{-1} (Fig. 2) in agreement with earlier reports on cocoa seedlings (Hutcheon 1977; Raja Harun and Hardwick, 1988a; Joly and Hahn, 1989). However, high light intensity decreased P_N under water stress conditions (April).

The relationship of P_N to C_i was nearly linear (Fig. 3) and CO_2 compensation concentration was at approximately 100 ppm. The C_i/C_a ratio of 0.80/0.88 is characteristic of a C_3 plant. P_N was positively correlated with g_s (Fig. 4). Consequently, the fluctuations in g_s to environmental changes will be reflected in values of P_N. Because of the linear relationship of P_N and g_s, the C_i/C_a ratio remained relatively constant despite the seasonal or accession type variations. This mode of relationship, although widely reported in the literature (Farquhar and Sharkey, 1982) is rarely measured in the field (Marco et al., 1988). There was also no significant difference in C_i (ranging from 230 to 290 ppm) showing that it did not limit the net assimilation rate. The relationship of environmental variables and P_N in cocoa clearly demonstrated that the latter is influenced by both soil and atmospheric droughts.

ACKNOWLEDGEMENTS

We thank K. Vijaya Kumar for statistical analysis of data and Y. Srinivasa Bhat for technical assistance.

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